POPULATION STUDIES OF GRASS GRUB (*Costelytra zealandica*) AND BLACK BEETLE *(Heteronychus arator)* (COLEOPTERA: SCARABAEIDAE)

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SUMMARY: Population studies of grass grub and black beetle have revealed simple patterns of population determination. Populations fluctuate in response to variations in soil moisture and temperature. The upper limit to population growth is set by density dependent factors (larval mortality of grass grub and variation in natality of black beetle). Parasites and predators appear to be generally unimportant, but disease organisms may be potentially useful in the management of grass grub and black beetle populations.

Black beetle outbreaks occur sporadically following warm springs whereas grass grub tends to be a more persistent problem. In areas such as the Waikato and Bay of Plenty where both species can occur as pasture pests, years in which the weather is favourable for black beetle population growth are unfavourable for grass grub. Population models have been developed which accurately describe the general patterns of grass grub and black beetle population change and can account for the observed effects of varying the application time of transient soil insecticides.

INTRODUCTION

The widespread use of DDT and other organochlorine insecticides in the 1950s and 60s provided effective control of the major soil-dwelling insect pests of New Zealand pastures. Research on pasture pests was minimised during this period (Given, 1968; Pottinger, 1973). Since the banning of DDT and most other organochlorines from farm use in 1970 no completely satisfactory chemical control has been available (Trought, 1979). Pasture pest control is now forced to rely on the integrated use of a range of control measures. This has placed renewed emphasis on population studies designed to provide the quantitative base essential for the development of effective pest management systems, in which all suitable tactics are utilised in a compatible and environmentally acceptable manner to maintain pest populations at levels below those causing economic injury (Pottinger, 1967, 1973, 1975; East, 1979; Kain, 1979).

This paper reviews progress in population studies of two scarabs, the native grass grub *(Costelytra zealandica* (White) (subfamily Melolonthinae) and the introduced black beetle *(Heteronychus arator* (Fabricius) (subfamily Dynastinae)). The root-pruning larvae of these species can cause severe losses in pasture production and they were rated as New Zealand's first (grass grub) and third (black beetle) most important pasture pests by Pottinger (1975).

POPULATION ECOLOGY OF GRASS GRUB

Grass grub has both the greatest range of ecological tolerance and the widest geographical distribution of New Zealand melolonthines (Given, 1952) and has profited from the modification or removal of the original vegetation and its replacement with exotic grasses and clovers, especially white clover (*Trifolium repens* L.) (Kain and Atkinson, 1977; East, Kain and Douglas, 1980). It is now a major pasture pest on free-draining soils throughout New Zealand, with the exception of the area north of the Waikato.

Life table studies over five grass grub generations from 1968-73 on the Takapau Plains in southern Hawkes Bay (Kain, 1975), shorter-term studies in Canterbury (Kelsey, 1951; East, 1972) and Nelson (Farrell, 1972), and subsequent observations in the Waikato and central North Island (East, unpublished information) have revealed a simple system of population determination. Population fluctuations between generations are largely determined by the density independent mortality of first- and second-instar larvae between December and February, which is inversely related to summer soil moisture when this declines below wilting point (Kain, 1975). Desiccation, exposure to high soil temperatures during summer droughts, and starvation may all contribute to this summer larval mortality. In some areas, e.g., Takapau, the influence of late winter rainfall on the mortality of fully fed larvae and prepupae may also influence population changes.

Adult dispersal is unimportant because the adult females do not fly from the areas they occupied as larvae until they have laid most or all of their eggs. Natural enemies also appear to be unimportant except in localised areas, with the possible exception of diseases (see below). In the absence of unfavourable extremes of weather, grass grub populations increase steadily over several generations until they reach the level where the larvae severely deplete their food supply. Population regulation is then effected by the mortality of second- and third.instar larvae in autumn and winter. This mortality arises from aggressive interactions between larvae and is strongly density dependent above a threshold density which varies between generations. Kain found a direct linear relationship between this threshold density and pasture growth in autumn and winter, which is a measure of the larval food supply. The population dynamics of grass grub revealed by these studies may represent a basic pattern for root-feeding pasture scarabs (East, 1979).

POPULATION ECOLOGY FO BLACK BEETLE

Black beetle is an African species which has been present for about 45 years in northern New Zealand, where it is at the limit of its climatic tolerance. It is confined to areas with a mean annual screen temperature ≥ 12.8°C, i.e., from the Waikato and Bay of Plenty northward with a southward coastal extension of its range to northern Taranaki and Gisborne (Watson, 1979). Black beetle outbreaks occur sporadically in New Zealand and are closely associated with above-average spring temperatures (Watson, *op. cit.).* This reflects the relatively high temperature requirements of black beetle, e.g., adult flight, oviposition, feeding and egg and larval development cease when ambient temperatures decline below 15-17°C (King, Mercer and Meekings, 1981a; Watson, unpublished information). In contrast, grass grub adult flight and egg and larval development do not cease until temperatures fall to about 5-10°C (Kelsey, 1968; Wightman, 1979a).

Life table studies over five black beetle generations from 1974-79 at the Otakanini research area, near Helensville, (King *et al.,* 1981b) and concurrent extensive population studies in Northland, Waikato, Bay of Plenty and Taranaki (Watson, 1979 and unpublished information; Watson and Wrenn, 1980) have revealed a close association between black beetle and the warm-climate adapted grasses paspalum *(Paspalum dilatatum* poir.) and kikuyu *(Pennisetum clandestinum* Hochst.). Pastures in which either of these two grasses is dominant are favourable habitats for black beetle throughout the year whereas pastures based on temperate species such as Ryegrass (*Lolium perenne* L. provide favourable habitats only during spring and summer, when larval development occurs. Infestation of ryegrass pastures depends on immigration of adult females in spring from sites where they have overwintered on paspalum or kikuyu.

Intergeneration population fluctuations in paspalum-dominant pastures are largely determined by the mortality of larvae between December and February, and variation in natality, which is the difference between the expected egg population, calculated from estimates of the resident population of adult females in September prior to oviposition and their average fecundity, and the observed egg population. Summer larval mortality is density independent and is directly related to the cumulative thermal units above 15°C in the previous spring (King *et al.,* 1981c). Warm springs allow earlier oviposition, more rapid egg and larval development and consequently greater survival over summer. Variation in natality is apparently involved in population regulation as well as population fluctuations, possibly because of density dependent dispersal of adult females in spring prior to oviposition (King *et al.,* 1981b, c). Unlike grass grub, black beetle is highly mobile in the adult stage and may undergo extensive dispersal flights in both autumn and spring. This allows much greater scope for density dependent dispersal (Taylor and Taylor, 1977; Taylor, Woiwod and Perry, 1978; Taylor and Woiwod, 1980) in black beetle than in grass grub.

In years with warm springs favourable for black beetle, populations and flight activity tend to be high throughout most of this species' geographical range in New Zealand with widespread colonisation of temporary (larval) habitats such as ryegrass-based pastures. Black beetle causes pasture damage throughout large areas of its range in these outbreak years. In cooler years populations tend to become localised in nucleus areas of paspalum or kikuyu on free-draining soils, which act as refuges until the recurrence of favourable weather.

The last serious black beetle outbreak in New Zealand occurred in the early to mid-1970s. Our present knowledge of black beetle population dynamics has come from studies conducted during the decline of this outbreak and several subsequent years of low populations throughout most of the species' range (King *et al.*, 1981c). Studies during the initial phase of an outbreak period will probably modify and increase our understanding of the population ecology of this pest.

POPULATION MODELS

Using k-values (Varley and Gradwell, 1970), grass grub population models can be expressed in the form

$$\log N_{n+l} = \log N_n - k_2 - k_3 + \log (RF) - k_l$$

where N_n and N_{n+1} are the population densities of larvae in early autumn in generations n and n + 1 respectively, k_l is summer mortality (eggs to second-instar larvae), k_2 is autumn and winter mortality (second- and third.instar larvae), k_3 is spring mortality (prepupae to teneral adults), R is the proportion of adults that are females and F is fecundity.

Models of this form based on life table data have given reasonably accurate simulations of grass grub populations in southern Hawkes Bay (Kain, 1975). Calculations of summer mortality (k_l) were based on the inverse linear relationship between larval mortality and soil moisture. Since long-term gravimetric soil moisture records are not available for most areas of New Zealand, it is preferable to use standard meteorological data to estimate k_1. For example, percentage mortality (M) between eggs and second-instar larvae on Horotiu sandy loam soils in the Waikato is a function of the available soil moisture calculated from the weather records of the Rukuhia Research Station (East, unpublished information) :

$$M = 47.3 + 1.38\, D \qquad r^2 = 0.91$$

where D is the number of days of soil moisture deficit between December and February, determined by calculating the water available to pasture each day as stored soil moisture from daily rainfall records and Thornthwaite's formula for potential evapotranspiration, using the method described by Coulter (1973) and assuming a soil moisture capacity of 102 mm for this soil type (Gradwell, 1968). If this relationship is used to predict summer mortality, k_l is given by

$$k_l = -\log (1.00 - 0.01\, M) = -\log (0.527 - 0.0138\, D)$$

Using parameter values observed by East (1972) and Kain (1975), if spring mortality is assumed to be constant at 37% (lea = 0.20), R = 0.50, and F = 14 eggs per female, the model for grass grub populations (expressed as numbers per m^2) on Horotiu sandy loams is

$$\log N_{n+l} = \log N_n - k_2 + 0.645 + \log (0.527 - 0.0138\, D)$$

Mortality of larvae during autumn and winter (k_2) is a slightly over-compensatory density dependent mortality above a threshold density (T) of larvae in autumn (East, 1972; Kain, 1975), given by

$$k_2 = 1.10 \log N_n - \log T$$

$$k_2 = 0 \text{ if } N_n^{1\text{-}10}\ T$$

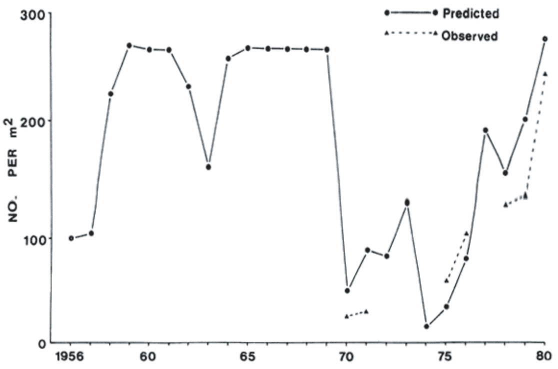

FIGURE 1. *Predicted and observed autumn larval populations of grass grub on Horotiu sandy loam soil in the Waikato (see text).*

Figure 1 shows grass grub populations for the period 1956-80 predicted by this model with D calculated from Rukuhia Research Station weather records, initial population density assumed to be 100 per m^2, and T to be 200 per m^2. These predictions show reasonable agreement with the average populations in 0.2-5.0 ha study plots within two adjacent farms on this soil type at Rukuhia observed by Kain (1975) in a single plot in 1970-71 and East (unpublished information) in 3 to 6 plots in 1975-76 and 1978-80. It is also known that the preikted population crash occurred in toe 1969-70 summer when Kain (1975) recorded a population decline from 289 eggs per m^2 in December to 26 second-instar larvae per m^2 in February (91 % mortality) during a severe drought. In addition, grass grub populations on this soil type are known to have been high on farms where DDT was not used during the late 1960s, when summer rainfall in the Waikato was consistently at or above average, and low during a succession of dry summers in the early 1970s, from the observations of farmers, farm advisory officers and research workers, including the authors. The predicted populations reach the levels shown in Figure 1 from 1961 or earlier if the assumed initial population in 1956 10 per m^2, because of the density dependent action of k_2. In practice grass grub populations are not as stable as this model predicts during periods of favourable weather, as in the mid-late 1960s, but as more information becomes available from ongoing population studies it should be possible to refine the model to allow for such factors as post-outbreak population declines which may occur before the onset of unfavourable weather (East and Kain, 1981), more accurate calculations of potential evapotranspiration than Thornthwaite's method, and variations in the threshold density for k_2 with autumn pasture production, which can also be calculated from the number of soil moisture deficit days (Baars and Coulter, 1974). Other factors such as different soil types, the effects of late winter rainfall on k_3 (Kain, 1975) and genetic factors (Given, 1968) may also be included.

The threshold population density at which grass grub populations begin to cause pasture damage varies with soil moisture, e.g., it is much higher in irrigated than in non-irrigated Canterbury pastures (East and Pottinger, 1975). Similar differences occur between wet and dry years in areas such as the Waikato, where populations of 100-150 or more oer m2 are potentially damaging on Horotiu sandy loams (East, unpublished information). The predicted populations in Figure 1 and similar simulations over a longer period suggest that grass grub populations on this soil type will frequently exceed this damage threshold level, except during exceptional spells of unfavourable weather such as the unusually long sequence of dry summers in the early 1970s.

Figure 2 compares the fluctuations of predicted grass grub populations (Fig. 1) around the damage threshold with the fluctuations of predicted black beetle populations in paspalum pastures given by King *et al.* (1981c), calculated from the model

$$\log N_{n+1} = 0.24 \log N_n + 0.95 + 0.008\ U$$

where N_n and N_{n+1} are the February black beetle larval populations (number per m^2) in generations n and n + 1 respectively, and U is the number of thermal units above 15 °C in the spring (September to November) between generations n and n + 1. This model is based on the inverse relationship between summer larval mortality and U and the density dependence of variation in natality observed in the life table study (King *et al.,* 1981 b, c). All other age-specific mortalities, sex ratio and fecundity are assumed to be constants equal to the average of the observed values. Using screen temperature records from the Woodhill Forest meteorological station, the model correctly predicted 80% of the recorded black beetle outbreak years in northern New Zealand since the mid-1950s, when black beetle first became a serious problem (King *et al.,* 1981c). While it was necessary to assume an initial population density to carry out this simulation, the predicted populations were identical within 3 generations regardless of the initial population, because of the density dependent factor in the model.

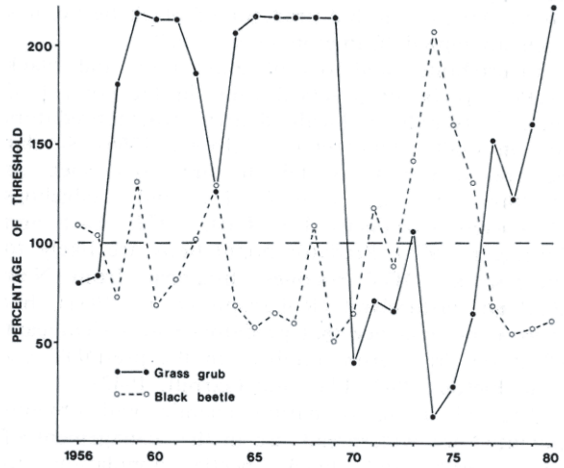

FIGURE 2. *Predicted late summer/autumn larval populations of grass grub in the Waikato (Fig. 1) and black beetle in the northern North Island (King* et al., *1981c) expressed as percentages of threshold densities of* 125 *and* 55 *per m2, respectively.*

Black beetle outbreak years are characterised by February larval populations exceeding a threshold level of 55 per m^2 under paspalum (King *et al., op. dt.).* Fluctuations of predicted numbers around this threshold tend to form a mirror image of the fluctuations of predicted grass grub numbers around the damage threshold for this species on Horotiu sandy loam soils (Fig. 2). The unprecedented sequence of warmer than average years in New Zealand in the early to mid 1970s (NZ Meteorological Service, 1975) created very favourable conditions for black beetle population growth in the northern North Island but unfavourable conditions for grass grub in the Waikato, while the reverse applied in most years during the mid to late 1960s when summer weather in northern New Zealand was not exceptionally warm or dry. Black beetle outbreaks have not been recorded on Horotiu soils, but high populations were widespread in the early to mid 1970s and low numbers in the late 1970s on Mairoa ash soils in the western Waikato hill country and Kaharoa ash soils in coastal Bay of Plenty, while the reverse applied to grass grub (East and Watson, unpublished information). Since the early to mid 1970s were exceptionally dry and warm, the pattern of grass grub and black beetle population change in the 1950s and 1960s (Fig. 2) is more likely to represent what will occur in future. On favourable soil types in the Waikato grass grub is likely to be a persistent problem, as it is further south (East, 1972; Kain, 1975), whereas black beetle outbreaks in northern New Zealand are likely to be sporadic, occurring perhaps once or twice a decade and typically lasting for 1 -2 years.

NATURAL ENEMIES

Since the patterns of grass grub and black beetle population change can be predicted successfully by simple models in which population fluctuations are determined by physical factors and the upper limit to population growth is set by density dependent intraspecific processes (larval competition and adult dispersal), these factors are probably dominant in population determination. This suggests that natural enemies of grass grub and black beetle are relatively unimportant at present. In contrast their potential importance is considerable, since the use of natural enemies in integrated control programmes has greatest application for pests whose population dynamics place them in an intermediate position on the r-K continuum (Southwood, 1977; Huffaker, Rabb and Logan, 1977). Kain (1979) pointed out that most New Zealand pasture pests are intermediate between the r and K extremes and their natural enemies should therefore receive more attention.

Parasites appear to offer little scope for Use in integrated control of grass grub and black beetle. The only insect parasite recorded from grass grub, *Proscissio cana* Hutton (Diptera: Tachinidae), is rare or absent in open pastureland (Thomas, 1963; Brown, 1966) and is dependent on the presence of 2-year life cycle grubs (Merton, 1980), which only occur commonly in lowland areas in the southern South Island (Stewart and Stockdill, 1972). Black beetle has no known insect parasites in New Zealand. Attempts to fill this gap in the natural enemy complex of grass grub and black beetle with introduced parasites have been unsuccessful (Cameron, Valentine and Butcher, 1979).

A range of predacious invertebrates are known to occur in New Zealand pastureland. While recent studies (Robertson and Pottinger, 1979; Robertson, Firth and Davison, 1981) have shown that predation by elaterids, carabids and staphylinids exerts a significant influence on populations of soldier fly *(Inopus rubriceps* Macquart (Diptera: Stratiomyidae), a pasture pest in the northern North Island, the few quantitative studies which have been carried out suggest that predators of scarab pests are generally unimportant in improved pastureland. Laboratory and field studies by East (1972) showed that while larvae of *Metaglymma monilifer* Bates, *Megadromus antarcticus* (Chaudoir) (Coleoptera: Carabidae) and *Ectenopsis lutuienta* (Hutton) (Diptera: Tabanidae) were voracious predators of third-instar grass grub larvae, they occurred in insufficient numbers in Canterbury pastureland (usually less than 0.5 per m^2) to influence grass grub populations significantly. East concluded that predation by two smaller predators, *Zeianion morbosus* (Hutton) (Chilopoda: Geophilidae) and *Xantholinus iabralis* Broun (Coleoptera: Staphylinidae), which readily preyed on grass grub eggs and first-instar larvae and occurred in populations of up to 46 per m^2 for the centipede and 18 per m2 for the staphylinid, did not significantly reduce the rate of grass grub population increase. Predation by *Z. morbosus* appeared to be buffered by the abundance of earthworms and other alternative prey. *X. labralis* was confined to the upper 5 cm of the turf, above the zone where most grass grub eggs and first-instar larvae occurred. Kain (1975) observed that adults and larvae of *Thyreo cephalus chloropterus* (Erichson) (Coleoptera: Staphyiinidae) and larvae of *Conoderus exsul* (Sharp) and *Ctenicera* sp. (Coleoptera: Elateridae) readily consumed grass grub eggs and larvae in the laboratory, but considered that populations of these and other invertebrate predators were too low in Hawkes Bay pastureland for predation to be an important mortality. Farrell (1972) found no evidence for significant predation on grass grub by *T. ch!oropterus* or *C. exsul* in Nelson pastureiand, despite the presence of the latter species in populations of up to 40 per m^2, while Cameron *et al.* (1979) stated that these two predators do not occur in sufficient numbers in the area infested by black beetle to contribute to the control of this pest. *T. orthodoxus* (Olliff) is locally common within this area and readily feeds on black beetle eggs, larvae and pupae (Butcher, 1979), but populations of all predators were low in the areas where the studies of King *et al.* (l981b) were conducted and precation on black beetle populations appeared to be insignificant. The introduction of *Sea rites* sp., a South African carabid predator of black beetle, has been attempted (Cameron *et al.*, 1979).

Invertebrate predators of grass grub and black beetle may be of practical value in the control of these pests only in localised areas where predators are unusually abundant (e.g., Brown, 1966). Similar remarks apply to vertebrate predators such as starlings *(Sturnus vuigaris* L.) and hedgehogs *(Erinaceus europaeus* L.) (East, 1972; East and Pottinger, 1975). Predator populations are likely to increase as DDT residues disappear from New Zealand pastureland (Robertson *et al.,* 1981), but there is no evidence that predators had a significant effect on grass grub numbers in the pre-DDT era (Dumbleton, 1942; Flay and Garrett, 1942).

The only group of natural enemies with obvious potential for widespread use in the management of grass grub and black beetle populations is disease organisms. Microsporidian protozoans were apparently suppressed by the effects of the widespread use of organochlorine insecticides on their hosts (Kain, 1979). Recent studies suggest that *Nosema* spp. and *Mattesia* sp. may now contribute to both regulation and fluctuations of grass grub populations in some areas (Miln, 1978, 1979) and may be responsible for post-outbreak population collapses (Miln, pers. comm.; East and Kain, 1981). A coccidian, *Adelina* sp., may influence variation in black beetle natality in some areas and hence both population regulation and fluctuations (King and Mercer, 1979; King *et al.,* 1981b). Further research is necessary to clarify the role of these protozoan diseases and recently discovered viruses (Longworth and Archibald, 1975; Dearing *et al.,* 1980) in grass grub and black beetle population dynamics.

PRACTICAL VALUE OF POPULATION STUDIES

Major advances have been made at research level in the development of pest management systems but similar advances have yet to be made in practice (e.g., Waters and Stark, 1980). Despite the lack of proven pest management systems, this approach is likely to be increasingly important in future for the control of many insect pests, including New Zealand pasture pests (Kain, 1979). Population studies provide one of the cornerstones of the development of pest management systems (East, 1979; Kain, 1979), alongside other areas of research such as assessment of the short and long term effects of control measures on both pest populations and pasture production.

Although the grass grub and black beetle population models described above are at a crude, initial stage of development, they can be used in association with population monitoring techniques (Kain, Holland and Atkinson, 1979; Watson, Marsden and Townsend, 1980) to determine the need for control measures. The sedentary nature of grass grub infestations allows population prediction to be based on the numbers present in the previous generation (East and Kain, 1981), which could be used with the calculation of summer soil moisture levels from weather records to determine the need for control of autumn larval populations. Similarly, knowledge of spring adult populations (Watson *et al.,* 1980) and predictions of summer larval mortality from spring temperature records could be used to rationalise insecticide applications against black beetle in early summer. In addition to population prediction, studies of the key mortalities responsible for population change may lead to the development of methods of manipulating these mortalities and hence pest populations, e.g., the use of summer grazing management to control grass grub (East and Willoughby, 1980).

These models are also useful for evaluating control measures, and can account for the problems of controlling grass grub with the transient soil insecticides which have replaced DDT and the effects of varying application time (Kain, 1975; East, 1979; East and Kain, 1981). Similarly, the above model for black beetle populations can be used to compare the effects of spring (September-October) and early summer (December) applications of transient soil insecticides. If the insecticide is assumed to kill 85 % of the population (k = 0.82), addition of this mortality to the black beetle model gives

$$\log N_{n+1} = 0.24 \log N_n + 0.75 + 0.008\, U$$

for spring applications, which precede and are therefore compensated by the density dependent variation in natality, and

$$\log N_{n+1} = 0.24 \log N_n + 0.13 + 0.008\, U$$

for early summer applications, in which the insecticidal mortality occurs after the density dependent factor.

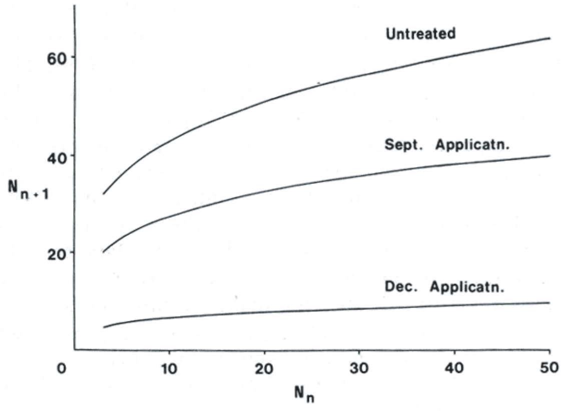

FIGURE 3. *Simulated effects of an 85 % insecticidal mortality on black beetle populations when application time is before (September) and after (December) oviposition (see text). N_n and N_{n+1} are the February larval populations (no. per m^2) in generations n and n + 1.*

Assuming favourable conditions for population growth (U = 55 ° days), the later treatment is clearly superior (Fig. 3). This is consistent with observations in field trials that post-oviposition applications of the transient insecticides diazinon, isazophos and terbufos in December gave a much higher level of control than pre-oviposition applications in September (Watson and Webber, 1976).

With further refinements it may be possible eventually to use these population models in more complex simulations, especially as knowledge of relationships between pest populations and production losses and the development of realistic models of pastoral systems (Wright *et al.,* 1976; Baars, 1980) proceed. Wightman (1979b) has proposed an energetics approach to assessing losses caused by pasture pests but in our opinion this is circuitous. The effects of pests on production can readily be estimated directly (e.g., Kain, 1975) without recourse to energetics studies, which may merely increase the chances of serious errors. In discussing energy flow studies, Macfadyen (1967) pointed out that "The final unknown in so many of these studies is of course the extrapolation of laboratory data to field conditions which in many cases may lead to the largest errors of all and make certain refinements irreicvant." The predictive powers of the grass grub and black beetle models even in their present crude forms and other benefits of population studies (East, 1979) underline the practical value of our approach. The failure to initiate population studies of New Zealand pasture pests earlier has probably delayed the development of successful pest management strategies (Pottinger, 1967).

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