Starling (Sturnus vulgaris L.) predation on grass grub (Costelytra zealandica (White), Melolonthinae) populations in Canterbury

R. East & R.P. Pottinger

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ABSTRACT

The main stages of the grass grub's life cycle available to starlings are third-instar larvae (autumn and winter) and adults (spring). Starlings were observed to concentrate their probing within localised areas of high grass grub density during autumn and winter, but the birds appeared to probe randomly for grubs within these areas. Average starling numbers were 1711.5–2915.4 starling-hours per ha per day during autumn and winter in 0.25- to 0.8-ha plots in an area of irrigated pastureland at Winchmore containing an isolated grass grub infestation near a large starling roost. Exclusion studies in this area revealed that starlings inflicted mortalities of 40–60% on medium (400–600 per m²) and high (> 1000 per m²) third-instar grass grub populations between March and July and that this mortality prevented medium grass grub populations from increasing. Observational studies at Winchmore showed that starling feeding effort in 0.25- to 0.40-ha areas increased markedly when local grass grub density exceeded a threshold of approximately 150–200 per m² in the top 2.5–3.0 cm of turf (a total population density of about 300–380 per m²).

In three other study areas, which were more typical of Canterbury pastureland, average starling numbers during autumn and winter ranged from zero to 152.1 starling-hours per ha per day and exclusion of starlings did not significantly influence grass grub mortality. Starling predation on grass grub adults apparently has a negligible effect on grass grub populations.

In the area of high predation at Winchmore, starling predation caused strongly density dependent mortality of grass grub populations over the range of densities from approximately 250–750 third-instar larvae per m². This predation, in combination with irrigation, high stocking rates, and grazing management which encouraged starlings to feed in infested paddocks, gave effective biological control of grass grub by preventing the population density from increasing above a level which caused moderate pasture damage in autumn but did not affect spring pasture production. Biological control of grass grubs by starlings may be possible only in localised areas with very high starling numbers.

CONTENTS

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I. INTRODUCTION

After the banning of DDT because of residues in pastoral produce, grass grub control has entered a new era, and there is no immediate prospect of another cheap, preventive control measure (Kain & Atkinson 1970). The emphasis is now on the use of both chemical and cultural controls, and the possibility of biological control is attracting new interest. Past attempts at biological control of grass grub, which have concentrated on the introduction of parasites of melolonthines from other countries, have been unsuccessful.

The natural enemies already present in New Zealand have been neglected, and the object of this study was to assess the magnitude and significance of predation by starlings on grass grub populations in Canterbury.

II. STUDY PLOTS

Five study plots were established as follows:

Winchmore plot 1: 0.8 ha of 11-year-old, border-dyked, flood-irrigated pasture on a Lismore stony silt loam at Winchmore, mid-Canterbury. This plot was situated on a 28 ha property of irrigated pastureland within 0.8 km of a large autumn and winter starling roost.

Winchmore plot 2: 0.4 ha of 8-year-old, border-dyked, flood-irrigated pasture, 8 km from Winchmore plot 1 and on the same soil type.

Winchmore plot 3: 0.25 ha of pastureland on the same property as Winchmore plot 1.

Weka Pass plot: 0.8 ha of 3-year-old, unirrigated pasture at Weka Pass, North Canterbury, on a Huihui soil.

Lincoln plot: 1.6 ha of 4-year-old, unirrigated pasture on the Lincoln College Research Farm, on a Templeton silt loam.

III. AVAILABILITY OF GRASS GRUBS TO STARLINGS

With the exception of the adult, all stages of the grass grub's life cycle are entirely subterranean (Kelsey 1951) and are available to starlings only when present in the upper 2.5–2.6 cm, which is the length of the starling's bill.

Fig. 1 — Life cycle and vertical distribution of grass grub at Winchmore, 1969.

Methods

To determine which stages of the life cycle are available to starlings, the vertical distribution of grass grubs was measured at approximately fortnightly intervals at Winchmore plot 1 throughout 1969 and 1970 and at the Lincoln plot in 1969. At Lincoln fifty 10-cm diameter soil cores were taken in each sample, using a soil corer developed by Kain & Young (1975). At Winchmore, where the stony soil precluded the use of corers, ten to twelve 15-cm spade squares were taken. Soil samples were sectioned, as they were taken, into depths of 0–2.5 cm and 2.5–25.0 cm. The grass grubs were extracted separately from the two levels, using the flotation and wet sieving method of Kain & Atkinson (pers. comm.) for the smaller stages and hand-sorting for the larger stages.

Results

The results of regular soil sampling in irrigated pasture at Winchmore are shown in Figs 1 and 2.
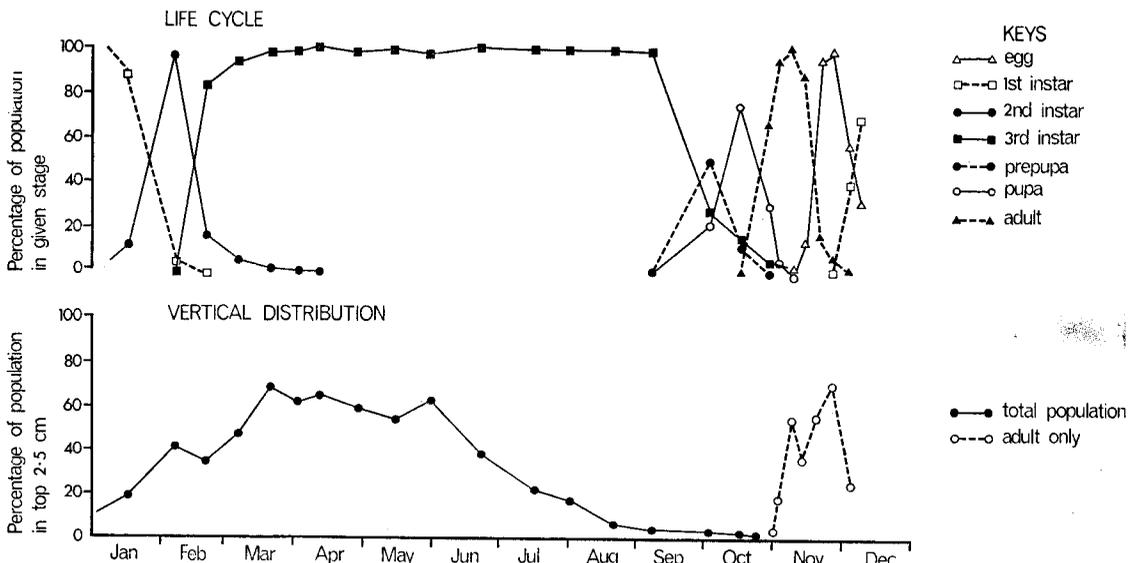

Fig. 2 — Life cycle and vertical distribution of grass grub at Winchmore, 1970.

The life cycle followed a similar pattern to that described by other workers (e.g., Pottinger 1968). Both the life cycle and the vertical distribution of grass grubs at Winchmore were very similar in the two years. Eggs were never found in the top 2.5 cm of turf. The gradual upward movement of larvae until 65–70% of early third-instar grass grubs were in the top 2.5 cm probably resulted from a continual search for fresh root material, larval feeding starting at the depths at which eggs were laid (5–20 cm). The decline in the proportion in the top 2.5 cm during February reflects a downward movement of larvae at the completion of the second instar, ecdysis taking place in cells at depths below 2.5 cm. Third-instar larvae completed their feeding and moved down to seek pupation sites in late winter (July–August). Prepupae and pupae were never found in the top 2.5 cm and were therefore unavailable to starlings; the only grass grubs at this level in September–October were a few third-instar larvae. Adults are crepuscular fliers and are active on the pasture surface during the night, spending the daytime in the soil and beneath surface vegetation and litter; sometimes more than 50% of the population is in the top 2.5 cm of the turf mat (including those sheltering above the surface).

The proportion of third-instar grass grubs in the top 2.5 cm at Winchmore in the period March–June altered little, if at all, with time of day, soil moisture, or soil temperature. Samples of third-instar larvae taken at any time of the day in autumn at Winchmore revealed large numbers of grubs in the top 2.5 cm. Extreme soil moisture contents in the top 2.5 cm at Winchmore between late February and May were 16.0% (very dry for irrigated Winchmore soils at this time of year) and 45.9% of dry weight (probably close to field capacity), the corresponding percentages of third-instar larvae in the top 2.5 cm being 47% and 59%. Frosts appeared to have no significant effect on the vertical distribution of third-instar larvae. Generally, only the top 0.5–1.0 cm of soil was frozen and this usually thawed before mid morning.

The vertical distribution of third-instar larvae at Winchmore was significantly influenced by population density (Fig. 3). The higher proportion in the top 2.5 cm at higher densities probably reflects a greater degree of upward movement of larvae in response to greater root depletion.

There was considerable overlap between developmental stages in the Lincoln population (Fig. 4), 20–25% of which overwintered as second-instar larvae in 1969, apparently because of a severe autumn drought. Field and insectary
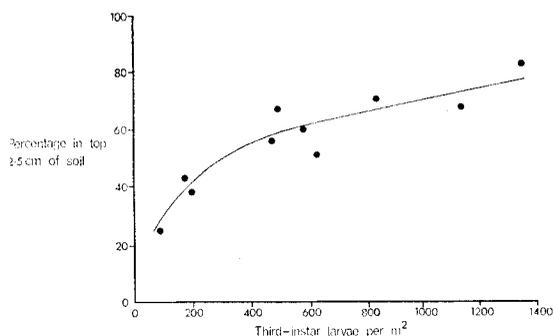
Fig. 3 — Relationship between vertical distribution and population density of third-instar grass grubs (March–April) in irrigated Winchmore pastureland. Each point based on a sample of 50–84 15-cm spade squares. Line drawn by eye.

observations indicated that all larvae that overwintered in the second instar had a 2-year life cycle, entering the third instar in September–October 1969, spending the subsequent summer, autumn, and winter in the third instar, and pupating in the spring of 1970. The drought conditions which prevailed at Lincoln in February, March, and April 1969 impeded the feeding, growth, and upward movement of larvae, which were stunted, sluggish, and largely absent from the top 2.5 cm until the drought broke in late April.

Discussion

The vertical distribution of third-instar grass grubs appears to be influenced only by extremes of soil moisture and temperature. Autumn and winter soil moistures in irrigated Canterbury soils may be generally too high to have any effect on the vertical distribution of grass grubs, as Kelsey (pers. comm.) observed that the vertical distribution of second- and third-instar C. zealandica at Lincoln was independent of soil moisture when the moisture content of the soil exceeded 16% of dry weight, which was the lowest level of autumn soil moisture encountered in this study on a similar soil type at Winchmore. Other workers have reported that the vertical distribution of scarabaeid larvae is influenced only by extremes of soil moisture (Milne 1956; Shorey & Gyrisco 1960), although Granovsky (1958) found that larvae of Phyllophaga spp. were highly sensitive to changes in soil moisture and moved up or down in the soil to reach preferred moisture conditions after each rainfall. Low soil temperatures during severe winter weather may force third-instar grass grubs to cease feeding, move down, and hibernate at depths of 25 cm or more (Miller 1921, 1945), but such behaviour does not occur in lowland Canterbury.
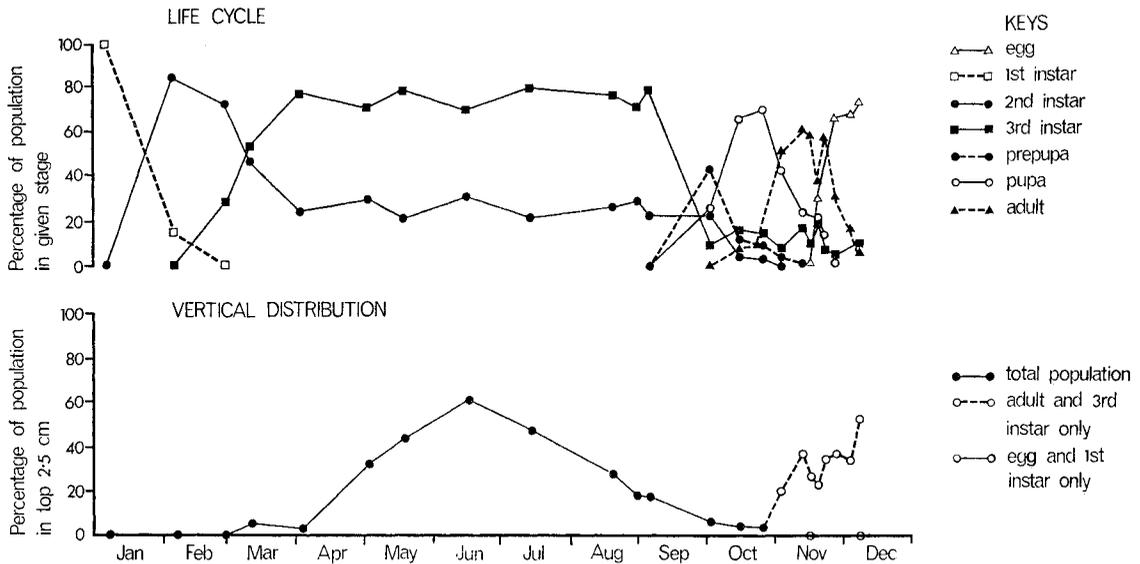
Fig. 4 — Life cycle and vertical distribution of grass grub at Lincoln, 1969.

The effects of drought on larval feeding, vertical distribution, and the length of the life cycle observed at Lincoln are similar to those recorded for other scarabaeids. Delayed larval development caused by food shortage, with consequent doubling or tripling of the length of the life cycle, has been recorded in other melolonthines (e.g., Tashiro *et al.* 1969), and larvae of several scarabaeid species are known to respond to drought conditions by moving down to depths of 10–15 cm or more and remaining there until the drought is broken, when they may return to the upper 5 cm within 24 h (Gambrell 1946; Milne 1956; Shorey & Gyrisco 1960; Maelzer 1961). Similar behaviour was earlier observed in *C. zealandica* by Kelsey (pers. comm.).

Figs 1, 2, and 4 show that grass grubs are available to starlings for two separate periods of the year: January to August, when larvae are present in the top 2.5 cm of soil in irrigated areas, and November to early December, when adults are abundant on and just below the soil surface. In unirrigated pastureland larvae may not appear in the top 2.5 cm in large numbers before March or April in most years, since unirrigated soils of the Canterbury Plains are normally very dry during January and February (Rickard & Fitzgerald 1970). The availability of third-instar larvae to starlings during March and April in unirrigated pastureland probably depends upon rainfall, wet periods increasing the proportion of larvae in the top 2.5 cm, and by softening the soil, facilitating starling probing.

Recent studies in Canterbury of the foods of the starling by Lobb & Wood (1971) in irrigated Winchmore pastureland, including the 28-ha farmlet where Winchmore plots 1 and 3 were situated, and by Coleman (1972) in unirrigated West Melton farmland have confirmed that two stages of the grass grub's life cycle, larvae and adults, are taken by starlings. Lobb & Wood found that third-instar larvae were taken in large numbers during autumn (March–May) and in smaller numbers throughout winter (June–August) and early spring (September–October), but apparently first- and second-instar grass grubs were not eaten. Possible reasons for the absence of the smaller larvae from the diet are discussed in section IV. Coleman found that third-instar grubs were taken from May to August, with a peak in late June and early July. The later initial and peak occurrences of larvae in the birds' diet in the unirrigated area reflect the effects of irrigation on the vertical distribution of grass grubs. Both studies showed that grass grub adults are a major item in the diet of adult and nestling starlings in November and December.

IV. OBSERVATIONS OF STARLING FEEDING BEHAVIOUR

Methods

Field observations — All field work was carried out on the 28-ha property of irrigated pastureland where Winchmore plots 1 and 3 were situated. During periods when a large proportion of the

grass grub population was in the upper 2.5 cm of soil, the feeding behaviour of starlings was observed through binoculars from either a permanent hide or a stationary motor vehicle.

Depths of starling probe-holes selected at random were measured by inserting a straight piece of fine straw into the hole. The distribution of probe-holes within localised areas was examined by counting the numbers of probe-holes in 36 contiguous 5-cm squares within 30-cm square quadrats.

Soil penetrability was measured using a hand-operated penetrometer with a stainless steel probe 6 mm in diameter and 2.5 cm long (Soil Test Inc., Chicago, U.S.A., model CT-421), which produced a probe-hole of similar dimensions to that made by a starling.

The rates at which starlings probed into turf were measured by observing with binoculars single birds for periods of 10 to 180 seconds. Measurement of probing rate was sometimes made difficult by the starling's habit of making several thrusts with the bill during a single probe. Even with powerful binoculars it was often difficult to determine when a probing starling shifted to a fresh site, and it was occasionally difficult to distinguish shallow probes from the act of picking up small objects from the surface. Judgment, therefore, was frequently subjective.

To observe the response of starlings to variations in grass grub density, plots of 0.40 ha were pegged out in the 28 ha containing Winchmore plots 1 and 3 on various occasions during autumn and winter, when third-instar grass grubs were present in the top 3.0 cm of soil. Each time a plot was marked out the density of grubs in the top 3.0 cm was measured by taking 100 soil cores 4.0 cm in diameter and 3.0 cm deep and extracting the grubs by hand-sorting. During the following 1–5 days an observation period of up to half a day was spent counting the number of

starlings which visited the plot and timing the length of each visit by a flock of starlings. Soil penetrability was measured by taking 10 penetrometer readings at the end of each observation period. Similar information was obtained at Winchmore plot 3, where grass grub density in the top 3.0 cm at the beginning and end of a continuous series of 4- to 13-day periods, soil penetrability, starling numbers, and probing rates were measured between March and June 1970. The lengths of visits by starling flocks to plot 3 were not timed, but starling counts were made every 5 min during observation periods of 1–12 h. The number of starling-hours spent on the plot during an observation period (N) was calculated from $N = \Sigma N_i/12$ (cf. Petrusewicz & Macfadyen 1970), where N_i is the number of birds in the ith count. The lengths of visits were estimated from the recorded counts by assuming that each count greater than zero represented a visit of 5 min, e.g., six consecutive counts greater than zero which were preceded and followed by zero counts were assumed to represent a single visit of 30 min. This procedure will tend to overestimate the average length of a visit, as no allowance is made for flocks leaving the plot and others arriving between two consecutive counts greater than zero, but any marked changes in the average length of a visit with variations in grass grub density should still be apparent.

The consumption of earthworms (*Allolobophora caliginosa* (Savigny) and *Lumbricus rubellus* Hoffmeister) by starlings was measured on two occasions in a 0.25-ha area at Winchmore by watching through binoculars birds feeding within 40 m of a hide. Capture of earthworms was easily observed, the birds often leaning back to pull large earthworms out of the soil. Individual birds were watched for periods of 2–6 min and the number of probes made and earthworms consumed in this period recorded. After the

TABLE 1 — Depths of starling probe-holes (cm)

Average soil penetrability (kPa)	No. measurements	Average depth	Range of depths
Captive starlings			
350– 700	110	1.6	0.3–3.3
700–1400	200	1.4	0.1–3.1
1400–2100	100	1.1	0.1–2.4
2100–2800	100	0.7	0.1–2.4
Field measurements			
700–1400	150	1.5	0.2–3.0
1400–2100	100	1.2	0.1–2.8
2100–2800	50	0.9	0.1–2.3

observations, grass grub and earthworm densities in the top 2.5 cm were measured in the area where the starlings had been feeding by taking ten 15-cm spade squares to a depth of 2.5 cm; soil penetrability was also measured.

Experiments with captive starlings — Wild adult starlings were kept in a cage 2.3 m × 0.8 m × 1.3 m within a screened insectary. The top and outward-facing walls of the cage were covered with wire netting and the inward-facing walls with hardboard. A 0.5-m by 0.3-m one-way mirror formed an observation window in one of the hardboard walls, so that it was possible to watch a starling feeding from a distance of 30–50 cm. A total of five starlings was used, no more than two being kept at any one time. All birds settled down in captivity after 2–3 days. They were fed minced beef, and occasional mealworms, earthworms, grass grubs, and bird seed *ad libitum.*

Pieces of undisturbed turf known to contain grass grubs were collected from areas of irrigated pasture at Winchmore by driving a stainless steel frame 7.5 cm high and 30 cm square into the soil. The grass was clipped to a height of 1.0–1.5 cm and one penetrometer reading taken. The square of turf within the metal frame was placed inside the cage containing a single starling and the number of grass grubs captured was recorded while the bird made 100–150 probes. The turf was then removed and the number of grass grubs remaining in the top 3.0 cm determined by careful hand-sorting. In some experiments the depths of 10 randomly selected probe-holes were measured before counting the remaining grubs.

Third-instar grass grubs were used in all experimental work with captive starlings. To obtain a wide range of grass grub densities, grubs were seeded in some experiments with a 0.7-cm diameter cork borer. They were seeded in from the bottom to within 0.5–3.0 cm of the upper surface, as initial studies had indicated that the acute vision and highly inquisitive nature of starlings enabled them to learn rapidly to locate the position of grubs seeded in from the upper surface of the turf.

Experiments with captive starlings were also used to determine whether starlings probe randomly for grass grubs. Grubs were seeded into 5-cm square areas within 30-cm square pieces of turf (collected from grass grub-free areas), which were placed with a starling while it made 20–50 probes. The turf was removed and the number of probe-holes counted on a 6 × 6 grid of 5-cm squares.

Results

Starling probing behaviour — At Winchmore starlings were observed to probe infrequently for subterranean prey before March, when third-instar grass grubs appeared in large numbers in the top 2.5 cm of soil. During January and February the birds fed mainly by surface hunting, i.e., by walking across the pasture surface, often with the head well forward, and making a sudden forward dart, apparently to capture some small mobile insect. Starlings were also observed picking up small objects from the surface, turning over sheep droppings, and jumping a short distance into the air to capture aerial prey, with only occasional probing even when the soil had been softened by irrigation or rain. Probing became more prevalent during March and was the main feeding method in mid to late autumn and winter.

Depths of starling probe-holes are summarised in Table 1. The greatest probe depths were 3.0–3.3 cm, a little longer than a starling's bill. Few probes were deeper than 2.5 cm and the average was much less, confirming that grass grubs only in the top 2.5–3.0 cm are available to starlings. The average probe-hole depth decreased as soil penetrability increased, as would be expected. Penetrabilities of 350–700 kPa represent very soft turf, which was seldom encountered in the field, and penetrabilities of 700–1400 kPa were typical of turf in the Winchmore study area during periods of high soil moisture. Under these conditions most probe-holes were 0.9–2.4 cm deep, and the proportion fell from 85% to 32% as soil penetrability increased from 350–700 to 2100–2800 kPa, the latter value being typical of dry hard soil. Shallow probes (0.1–0.8 cm) were not accompanied by marked bill gaping and comprised 50–70% of all probes at penetrabilities of 2100–2800 kPa. Under these conditions captive starlings often made a rapid series of shallow probes, as though searching for a soft spot in the dry turf. Probe-holes deeper than 2.4 cm resulted when captive starlings made a series of rapid probes without withdrawing the bill.

Starling probing rates in the field at Winchmore, summarised in Table 2, ranged from 2.0 to 57.3 probes per min. Analysis of variance showed that the increase in average probing rate between March–April and May–June was highly significant (P < 0.005). This increase probably reflects a decline in the amount of food available to starlings over this period, so that the birds had to work harder in winter to obtain adequate nutrition. Average probing rates were lower on rain days (more than 0.2 mm) than on dry days in all months. This difference was significant for both March and May (P < 0.005) but not for

TABLE 2 — Starling probing rates recorded at Winchmore

Month	Rain days		Dry days		Total	
	No. observations	Average probes/min	No. observations	Average probes/min	No. observations	Average probes/min
March	96	20.6	74	27.1	170	23.4
April	23	18.9	122	26.0	145	24.9
May	37	26.0	74	33.3	111	31.1
June	7	30.7	51	34.2	58	33.9

April or June (P > 0.10). The tendency for probing rate to be lower on rain days may have resulted from a greater availability of food on these days, when the soil was softer and earthworms were driven from their tunnels by rain, so that the birds did not have to search as intensively as on dry days. Alternatively, it may have resulted from starlings making deeper probes in the softer soil on rain days and consequently spending longer, on average, over each probe.

Location of grass grubs by starlings — The results of experiments with captive birds are shown in Table 3. Grass grubs were seeded one to an occupied 5-cm square, and soil penetrability was between 700 and 1400 kPa in all trials. No more than two grubs were captured in any trial. Only in one of the 16 trials did the average number of probe-holes per 5-cm square differ significantly between squares which initially contained grass grubs and those which did not. In

this one trial the average was significantly higher in squares without grubs. There is little doubt that the starlings were probing randomly. The significant difference in trial 7 arose presumably by chance.

The distribution of starling probe-holes within localised areas of heavy probing in the field is shown in Table 4. Only 2 of the 14 distributions differed significantly from random, randomness being indicated by a variance : mean ratio of unity (Salt & Hollick 1946).

The distribution of third-instar grass grubs in the top 3.0 cm of a 0.25-ha area at Winchmore was initially even (Table 5), the variance : mean ratio being less than unity, probably as a result of aggressive interactions between feeding third-instar larvae within this area of high grass grub density. The distribution was indistinguishable from random at the lower population densities encountered in the last few samples.

TABLE 3 — Comparisons of distribution of probes by captive starlings with distribution of grass grubs within 30-cm square pieces of turf, including tests for significance of the differences between the average number of probe-holes in 5-cm squares with and without grass grubs

Trial	No. probe-holes	No. 5-cm squares containing grubs	Average no. probe-holes/5-cm square		t (34 d.f.)
			Squares with grubs	Squares without grubs	
1	19	5	0.800	0.484	1.031
2	46	5	1.800	1.193	1.002
3	41	5	0.800	1.193	0.903
4	35	10	0.900	1.000	0.316
5	39	10	1.400	0.962	1.123
6	44	10	1.000	1.308	0.833
7	43	10	0.800	1.346	2.328*
8	50	10	0.900	1.577	1.313
9	48	10	1.700	0.962	1.117
10	47	10	1.400	1.269	0.257
11	16	15	0.600	0.333	1.219
12	20	15	0.300	0.714	1.612
13	39	15	1.200	1.000	0.459
14	43	15	1.466	1.000	1.116
15	49	15	1.533	1.238	0.738
16	48	15	1.133	1.476	0.770

* Significant at 5% level

TABLE 4 — Means $(\bar{x})$ and variances (s^2) of counts of starling probe-holes in 36 contiguous 5-cm squares within 30-cm square areas at Winchmore

Date (1970)	Quadrat	$\bar{x}$	s^2	$s^2/\bar{x}$
18/3	1	4.305	3.989	0.926
	2	3.555	3.397	0.955
	3	3.000	8.800	2.933*
	4	3.333	3.085	0.925
3/4	1	0.888	0.902	1.016
	2	1.277	2.149	1.683*
	3	3.194	3.875	1.213
	4	0.972	1.456	1.498
11/5	1	1.861	2.294	1.233
	2	1.000	1.086	1.086
	3	1.694	1.353	0.798
15/6	1	0.583	0.478	0.820
	2	1.000	1.257	1.257
	3	1.000	1.314	1.314

* Significantly different from unity at 5% level

Effects of soil conditions on the capture of grass grubs — The results of experiments on the capture of grass grubs by captive starlings are shown in Figs 5 to 8 in the form of regressions of capture success (CS, grubs captured per 100 probes) on the initial grass grub density in the top 3.0 cm (N). The complete data are presented in East (1972). Polynomial regression analysis revealed that there was no significant curvilinearity in the regression for any soil penetrability class. The slope of the regression of CS on N, and hence the capture success at a given grass grub density, increased as the soil became softer, as would be expected, since the average dimensions of probe-holes increased with ease of penetration.

By combining the information on capture success of starlings probing for grass grubs at different grass grub densities with field measurements of grass grub density in the top 3.0 cm of turf, starling probing rates, and soil penetrability, the feeding rate of starlings can be calculated in terms of grass grubs per min. For example, the average May and June probing rate of 32.5 probes per min produces the lines in Fig. 9.

The relationship between feeding rate and grass grub density is assumed to be linear. As grass grub density increased the rate of increase of feeding rate would be expected to gradually decline and eventually become zero when feeding rate reached an upper asymptote, corresponding to the density where starlings spent all their time picking up and eating grass grubs with no time available for searching. At the highest grass grub densities encountered in the field in the top 3.0 cm in this study (700–800 per m²), the calculated feeding rates do not rise above four grass grubs per min. Captive starlings usually took no more than 1–2 sec to remove and eat a captured grass grub. At a feeding rate of four grubs per min the birds would, therefore, lose only 4–8 sec of searching time per min, and since feeding rates were usually well below this level, it appears a reasonable approximation to ignore "handling" time (Holling 1959b) over the range of densities occurring in the field. Fig. 9 shows that at a given grass grub density and probing rate, feeding rate increases as the soil becomes softer, and that at the same probing rate

TABLE 5 — Means $(\bar{x})$ and variances (s^2) of samples of grass grub population in top 3.0 cm at Winchmore (each sample consisted of 200 4.0-cm diameter soil cores)

Date (1970)	$\bar{x}$	s^2	$s^2/\bar{x}$
18/3	0.695	0.283	0.407*
26/3	0.490	0.271	0.553*
3/4	0.380	0.247	0.650*
20/4	0.345	0.267	0.774*
29/4	0.315	0.217	0.689*
11/5	0.250	0.198	0.792*
21/5	0.185	0.151	0.816
1/6	0.160	0.135	0.844
15/6	0.110	0.108	0.982

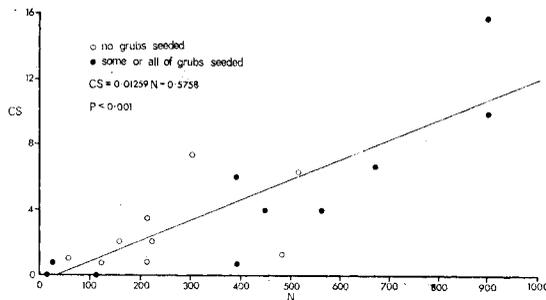* Significantly different from unity at 5% level

Fig. 5 — Relationship between number of third-instar grass grubs captured by captive starlings per 100 probes (CS) and number of grass grubs per m^2 in top 3.0 cm of turf (N) at soil penetrabilities of 350–700 kPa. P is the probability that the slope of the regression does not differ from zero. CS and N are expressed in the same units in Figs 6–8.

a given feeding rate can be achieved at lower grass grub densities the lower the average penetrability.

Accuracy of calculated feeding rates — The numbers of grass grubs destroyed by starlings in consecutive periods of 4–13 days were measured at Winchmore plot 3 using experimental field populations of grass grubs (section VI). All-day bird counts were made to count accurately the number of starlings feeding in plot 3. Grass grub density in the top 3.0 cm, soil penetrability, and starling probing rates were also measured. This information checks calculated feeding rates against field estimates of actual feeding rates. For example, from 13–17 March 1970, continuous all-day bird counts revealed that a total of 15 267.4 starling-hours was spent on plot 3.

Fig. 7 — Relationship between CS and N at soil penetrabilities of 1400–2100 kPa.

Grass grub density in the top 3.0 cm was 665.83 per m^2, averaging measurements made on 10 and 18 March. Average soil penetrability was 700–1400 kPa during this period. From the relationship given in Fig. 6, capture success is calculated as 4.79 grass grubs per 100 probes. The average probing rate was 16.9 probes per min, giving a calculated feeding rate of 0.809 grubs per min. The total number of grass grubs destroyed per m^2 is therefore calculated as (plot 3 was 2592 m^2 in area): $\dfrac{15\,267.4 \times 0.809 \times 60}{2592} = 285.91$. This

compares with the estimate obtained from the experimental field population of 219.72 grass grubs per m^2 removed from plot 3 by starlings in the period 11–17 March inclusive. The estimate

Fig. 6 — Relationship between CS and N at soil penetrabilities of 700–1400 kPa.

o no grubs seeded
● some or all of grubs seeded

CS = 0·00287N − 0·0155

P < 0·05
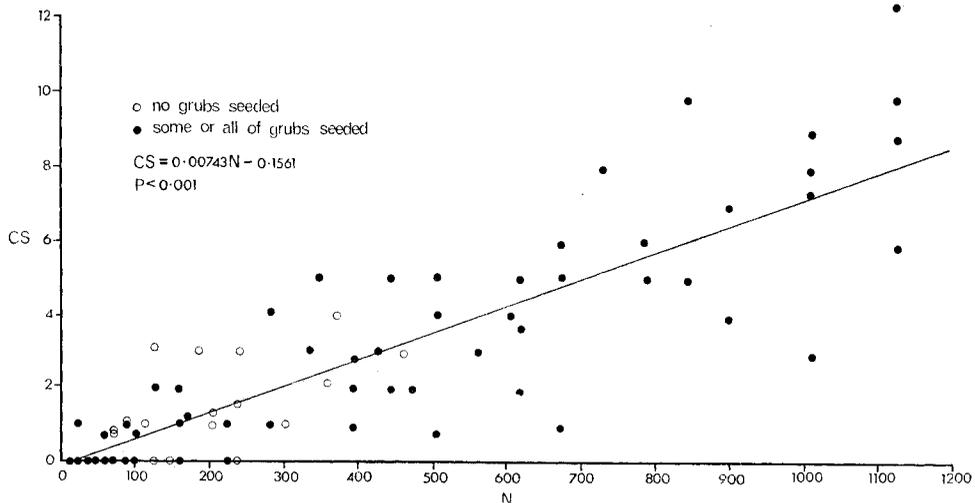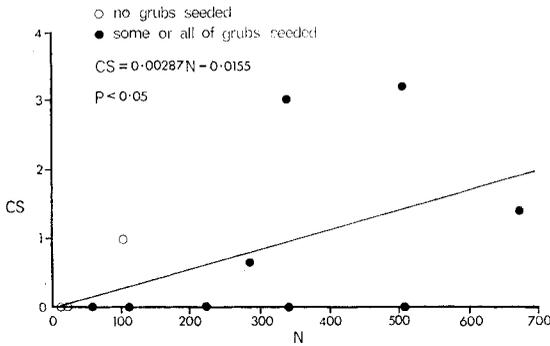

Fig. 8 — Relationship between CS and N at soil penetrabilities of 2100–2800 kPa.

Fig. 10 — Relationship between starling numbers and calculated feeding rate at Winchmore.

obtained from the calculated feeding rate does not allow for starlings which fed in the plot on 11 and 12 March, when counts were not made, and should therefore be greater than 285.91 per m². However, plot 3 was dry and hard (average penetrability 2105 kPa on 9 March) until 40.9 mm of rain fell on 13 and 14 March, softening the soil sufficiently for starlings to probe readily for grass grubs. Hence it is unlikely that the absence of bird counts for 11 and 12 March made a great difference to the estimate of predation mortality. The similarity of the two independent estimates shows that calculated feeding rates were at least of the same order as the actual feeding rates.

The response of starlings to grass grub density — Capture success in the 0.40-ha plots where the response of starlings to different grass grub densities was observed was calculated from the field measurements of grass grub density and soil penetrability, using the regressions in Figs 5 to 8. Probing rates were not measured during these observations and feeding rates (grass grubs captured per min) were calculated by assuming an average probing rate of 32.5 probes per min

(the average for observations at Winchmore in May and June), since almost all of this work was carried out during these two months. At Winchmore plot 3 the average of the initial and final densities was used to calculate capture success for each 4- to 13-day period, and feeding rates within each period were calculated directly from observed probing rates.

The Winchmore study area was often visited by flocks of tens and hundreds of starlings during autumn and winter. Starling counts (starling-hours per ha per day) appeared to be independent of the calculated feeding rate until it reached approximately 0.3–0.4 grass grubs per min, but increased rapidly as feeding rate increased above this level (Fig. 10) because of increases in both the number and length of visits by starling flocks. The average length of starling visits showed a similar relationship to feeding rate (Fig. 11). The complete data on which Figs 10 and 11 are based are given in East (1972).
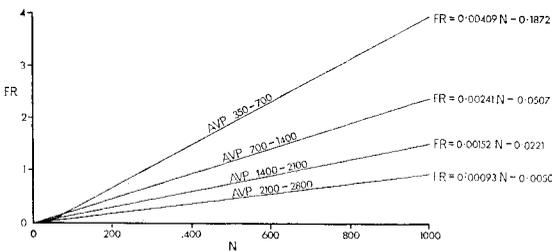

Fig. 9 — Relationship between calculated feeding rate of starlings (FR; grass grubs per min) and grass grub density in top 3.0 cm of soil (N; grubs per m²) at different average soil penetrabilities (AVP; kPa) and a probing rate of 32.5 probes per min.
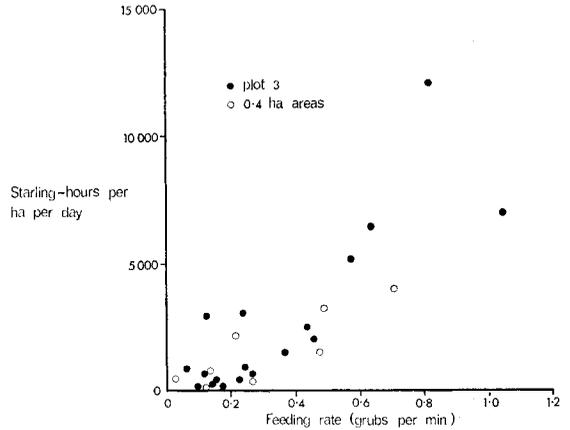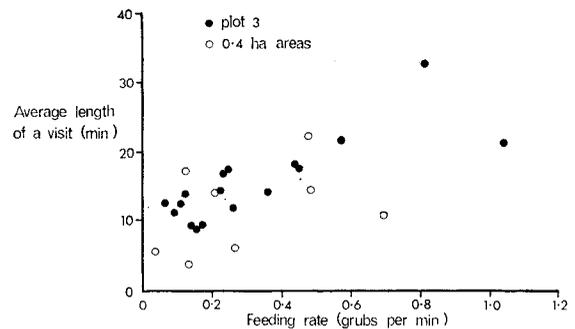

Fig. 11 — Relationship between average length of a visit by a flock of starlings and calculated feeding rate at Winchmore.

The average length of a visit by a flock of starlings to a 0.40-ha area when the calculated feeding rate was less than 0.3 grass grubs per min was between 5 and 10 min. At feeding rates of 0.3–0.4 grass grubs per min each starling would find, on average, one to four grubs in this time. Grass grubs were a highly preferred food of captive starlings and it is conceivable that the capture of only one or two in a 5- to 10-min period would be sufficient to induce the birds to remain in a 0.25- to 0.40-ha area and continue to search for grubs. Most of the predation by starlings on grass grubs at Winchmore occurred on or soon after rain days, when soil penetrability was between 700 and 1400 kPa and starling counts were high (section V). A feeding rate of 0.3–0.4 grubs per min corresponds with grass grub densities in the top 3.0 cm of approximately 150–200 per m², at average soil penetrabilities of 700–1400 kPa (Fig. 9). This represents a total population density of about 300–380 per m², calculated from the relationship between vertical distribution and density of third-instar larvae (Fig. 3). When local grass grub density in the Winchmore study area exceeded this level, starlings appeared to concentrate their feeding effort on grass grubs.

The average length of a visit by a flock to a 0.25- to 0.40-ha area seldom exceeded 25 min. Flocks often left areas of this size by their normal feeding movement over the pasture surface, birds at the back flying over the flock to land at the front. Frequently the entire flock flew off and settled to feed in an adjacent paddock, possibly because they had depleted the local grass grub density to below a profitable level or because they deliberately switched to another food to maintain a mixed diet, as Tinbergen (1960) postulated for titmice.

Consumption of earthworms — Field observations of the rate of capture of earthworms are shown in Table 6. Average soil penetrability and starling probing rate were 1137 kPa and 25.2 probes per min on 23 March and 1103 kPa and 34.1 probes per min on 18 June. Capture of grass grubs was calculated from the regression of capture success on grass grub density obtained with captive starlings at soil penetrabilities of 700–1400 kPa (Fig. 6) and combined with average

probing rate to calculate the rate of capture of grubs. Grass grub density and hence calculated feeding rate declined markedly between March and June. In contrast, earthworm density in the top 2.5 cm was approximately the same on the two observation days, suggesting that either a greater proportion of the earthworm population was in the top 2.5 cm in June or earthworm reproduction balanced mortality between March and June. Surprisingly, the number of earthworms captured per 100 probes was much higher in June, despite the similarity in earthworm density and soil conditions.

Discussion

Factors influencing starling predation on grass grubs — Starlings consume a wide variety of invertebrates in Canterbury pastureland, the occurrence of insect pests in the diet reflecting their seasonal abundance (Lobb & Wood 1971; Coleman 1972). Whether starlings feed on grass grubs when they are available probably depends on the starling's food preferences and the abundance of alternative prey. Fifteen to forty percent of first- and second-instar grass grubs were in the top 2.5 cm at Winchmore in January and February, but Lobb & Wood did not record grass grub larvae in the starling's diet until third-instars were available in March. This coincides with the starlings' change from predominantly surface hunting to predominantly probing observed in this study. During January and February the starling, apparently sampled the available subterranean prey from time to time, but concentrated on surface-dwelling prey such as the weevils *Hyperodes bonariensis* Kuschel and *Irenimus* spp., and the wheat bug (*Nysius huttoni* Wh.), which form the bulk of the starling's summer diet at Winchmore (Lobb & Wood 1971). It is well known that birds prefer larger food items within the size range of prey taken, so that the larger stages of an insect's life cycle are the stages susceptible to bird predation (e.g., Betts 1955; Tinbergen 1960; Mook 1963; Buckner & Turnock 1965; Mattson *et al.* 1968; Royama 1970). Whereas first- and second-instar grass grubs may be unattractive to starlings compared with the surface fauna which is abundant in irrigated pastures in summer and can be obtained with

TABLE 6 — Consumption of grass grubs and earthworms by starlings

Date	No. per m² in top 2.5 cm		Capture of earthworms		Calculated capture of grubs per h
	Grass grubs	Earthworms	per 100 probes	per h	
23/3/70	524.2	183.4	1.0	15.1	56.5
18/6/70	124.5	175.3	2.2	45.0	15.7

little or no probing, the much larger third-instar grubs are probably more attractive than small, hard-bodied insects such as weevils and wheat bugs.

Grazing management had a major influence on starling predation on grass grubs at Winchmore during autumn. Summer growth of irrigated pastures exceeds stock requirements, the excess production being conserved for autumn and winter feed by closing areas to grazing. On the 28-ha farmlet which contained Winchmore plots 1 and 3, 8 or 9 of the 11 paddocks had been closed to grazing for 3–12 weeks by early March and were moderately to very rank. The dense, rank pasture in most of these paddocks excluded starlings, which showed a marked preference for short, close-grazed pastures, as was also observed by Dunnet (1955), Boyd (1968), and Coleman (1972).

The paddocks of summer- and autumn-saved pasture were grazed rotationally during autumn and winter. Each paddock was grazed at a very high stocking rate (approximately 250 ewes per ha), for 1–2 h per day for the first 7–10 days and then for longer periods each day until the pasture was grazed very short. The paddock was then used as a run-off while the next one in the series was grazed. The starlings first entered a paddock during the initial grazings, usually arriving a few minutes after grazing began and leaving when disturbed by the sheep being driven off. Although counts were not made, it appeared that areas which had not been grazed for 2–3 months contained much larger numbers of surface-dwelling invertebrates, notably staphylinids, leaf hoppers (Jassidae), and small spiders, than samples from grazed areas (cf. Morris 1968). The starlings may have initially been attracted by the sudden availability of surface fauna disturbed by grazing. At first the birds fed mainly by surface hunting, often close to grazing sheep which the birds appeared to use as beaters. Once the pasture was grazed short the visits of starlings were independent of the presence of sheep and probing became the main feeding method.

Location of grass grubs by starlings — The starling locates subterranean prey by thrusting the closed bill into the soil and then partly withdrawing and opening the bill to widen the hole. The bird simultaneously looks into the hole to see if any prey are exposed. Lorenz (1949) was the first to describe this feeding technique, which he termed the "Zirkeln". He pointed out that the position of the eye directly in line with the bill opening, instead of well above it, as in most passerines, and the lateral compression of the section of the skull in front of the eyes, allow the starling to look directly into the hole it has made without withdrawing the bill. The lack of forehead allows the starling to slide the head forward very rapidly and grasp an exposed food item (Vik 1962).

The experiments with captive starlings showed clearly that the birds were unable to locate the positions of individual grass grubs before probing. Since the distribution of grass grubs in the top 3.0 cm of soil within an area of high grass grub density varied from even to random (Table 5), the random distribution of starling probe-holes among 5-cm squares observed in the field (Table 4) is a better strategy for locating grass grubs than a markedly clumped distribution of probes, which would reduce the chances of finding grubs. Other workers have reported random probing by birds searching for concealed prey (MacLellan 1958; Kahl 1964; Bengtson & Svennson 1968), although birds are quick to respond to visual signs of concealed prey, such as the entrances of earthworm tunnels or the ends of retreating worms (Heppner 1965; Heppleston 1971).

Although starlings apparently probe randomly for grass grubs, they concentrate their probing within areas of high grass grub density. Probe-holes made by starlings in autumn and winter at Winchmore were concentrated almost entirely within localised areas of 20–500 m^2, where grass grub population density was high enough to cause visible pasture damage in the autumn. Starling counts were much higher in grass grub-infested pasture than in adjacent grass grub-free areas (section V). Similar behaviour of starlings and other birds feeding on scarabaeid larvae in turf was noted by Raw (1951) and Carne & Chinnick (1957).

Starlings probably locate patches of high grass grub density by observing pasture damage. Grass grubs are concentrated within and close by areas of damaged pasture within a paddock (Kain & Atkinson 1970). After Winchmore pastures have been heavily grazed in the autumn pasture damage is no longer visible, but severely damaged areas are often revealed by turf pulling caused by sheep. Starlings may see localised areas of high grass grub numbers while pasture damage is obvious and continue to revisit these areas throughout autumn and winter. They may be capable of returning to the exact spot, since Croze (1970) found that carrion crows were apparently able to distinguish different areas within a featureless shingle beach. Alternatively, starlings could relocate an area previously heavily probed. Starlings may also locate local concentrations of grass grubs from the softness of the turf mat where grass grubs have damaged the roots, or by

initially adopting a random search until grubs are located and then restricting their search to the immediate vicinity of the discovery, i.e., adopting area-restricted searching (Tinbergen *et al.* 1967).

Gibb (1962) suggested that birds searching for concealed prey may use signs of previous attacks to tell them when an area has been fully exploited, but whereas the holes left in pine cones by the tits he studied usually indicated the successful capture of a prey, most starling probe-holes in turf do not. Starlings usually spend only a few minutes in a given patch of high grass grub density, and upward movement of grubs from below the 3.0 cm depth could replenish the supply of grubs in heavily probed, depleted areas. Therefore, the "predation by expectation" postulated by Gibb would not be expected to apply to starlings searching for grass grubs.

The response of starlings to grass grub density — At Winchmore starlings showed a marked behavioural numerical response (Buckner 1966, 1967) to grass grub density above the level where feeding rate exceeded 0.3–0.4 grubs per min. Similar hunting behaviour has been reported in other insectivorous birds, little interest being shown in a prey species until its density exceeds a threshold level (e.g., Gibb 1962, 1966; Beaver 1967).

Changes in the rate at which insectivorous birds consume a prey species can result from changes in the birds' perception, by which the birds learn the specific visual characteristics of the prey, i.e., from hunting by searching image (Tinbergen 1960; Dawkins 1971), or from changes in the location of the birds' hunting effort without change in their ability to detect prey. Birds can concentrate their hunting in the most profitable parts of their habitat by concentrating their search for prey in the immediate vicinity of a previous discovery, i.e., by area-restricted searching (Tinbergen *et al.* 1967), or by sampling and evaluating different areas (Gibb 1962; Royama 1970). Royama emphasised the use of locational cues by titmice searching for prey and questioned the validity of Tinbergen's (1960) searching

image hypothesis, but sometimes changes in the location of hunting effort and in the ability to detect prey may both be involved. Mook *et al.* (1960) found that when tits preyed on freshly emerged *Bupalus piniarius* L. moths on the forest floor, they not only increased the time spent hunting on the ground but also appeared to form visual searching images for *B. piniarius* moths on the ground. Some avian predators readily learn both the specific visual characteristics of a prey and where to find it (Croze 1970; Alcock 1973).

The concentration of hunting in the most profitable parts of the habitat is probably of major importance to birds searching for concealed prey. The problem faced by starlings searching for subterranean grass grub larvae is not whether they can detect camouflaged prey against a similar background (grass grubs are yellowish *white* and when exposed stand out against a background of soil), but whether it is profitable to probe randomly within localised concentrations of grass grubs. The profitability or rate of capture of grass grubs is directly proportional to grass grub density and inversely related to the resistance of the soil to a probe. When local profitability exceeded 0.3–0.4 grubs per min, the starlings responded by spending more time searching for grass grubs in that area and making more frequent visits to the area. Concentration of searching in the areas of greatest profitability has also been observed in titmice (Gibb 1958, 1966), woodpeckers (MacLellan 1958; Beaver 1967), and redshank (Goss-Custard 1970) searching for concealed prey. Flocks of starlings consistently revisit the same localised areas of farmland (Hamilton & Gilbert 1969; Coleman 1972), possibly because they remember areas which have proved profitable in the past and regularly revisit and sample them (cf. Croze 1970). Hamilton & Gilbert pointed out that the flocking action of starlings enables them to assess an area more accurately and quickly than if the birds fed as scattered individuals.

Consumption of earthworms — It is implied above that the length of time for which starlings probed in localised areas of pastureland depended

TABLE 7 — Daily energy requirements of an 80 g starling and yield from grass grubs and earthworms (metabolisable energy)

Date	Daily energy requirements (kJ/h)	Yield (kJ/h)		
		From grass grubs	From earthworms	Total
23/3/70	18.67	24.86	16.02	40.88
18/6/70	32.06	6.92	47.71	54.63

on the rate of capture of grass grubs, but other soil invertebrates exposed by probing are also consumed, and the feeding of starlings in localised areas may have been influenced by the availability and density of these alternative prey species. Apart from grass grubs the only abundant soil macro-organisms in the Winchmore study area were the earthworms *Allolobophora caliginosa, Lumbricus rubellus,* and *Octolasium cyaneum* (Savigny), the first two species occurring in large numbers in the top 2.5 cm of turf throughout autumn and winter. Earthworms are eaten regularly by starlings in Canterbury pastureland when soil moisture is high (Lobb & Wood 1971; Coleman 1972). Other major items in the starling's diet, such as adult weevils (*Hyperodes bonariensis, Irenimus* spp.) and the wheat bug, are found mainly on or above the soil surface and in cracks in the soil and are captured by surface hunting rather than by probing, which was the main feeding technique used by starlings at Winchmore during late autumn and winter.

Earthworms were not a favoured food of captive starlings, grass grubs and mealworms being preferred to the extent that, when a mixture of foods was available, no earthworms were eaten until all the insects had been consumed. Earthworms were readily eaten if no other food was available. Captive starlings probing into turf were never observed to reject grass grubs, but were frequently observed to reject earthworms, pulling them partially out of the soil and then dropping them and probing elsewhere. Earthworms may be rejected because their outer layer of mucus favours the adherence of soil particles, since earthworms were frequently rubbed several times against the floor of the cage, apparently to scrape off soil particles, before they were eaten. The low consumption of earthworms in the field in March, when grass grubs were available in large numbers (Table 6), may have resulted from rejection of earthworms, and it seems highly unlikely that the spatial distribution of the starlings' feeding effort would be influenced by local variations in earthworm density while third-instar grass grubs were readily obtainable.

Energetics — Energetics calculations based on the data on consumption of grass grubs and earthworms (Table 6) are given in Table 7. The average weight of wild starlings in autumn and winter is approximately 80 g (Coleman pers. comm.). The existence energy of an 80 g starling calculated from the equations given by Kendeigh (1970) is 100.06 kJ per day at 30°c and 185.22 kJ per day at 0°c. By assuming that existence energy (M) increases linearly with decreasing ambient temperature (T), which is not an unreasonable

assumption (Kendeigh 1969), the existence energy of an 80 g bird at any intermediate temperature can be determined from

$$M = -2.84T + 185.22$$

where M is in kJ per day and T in °c. Thompson & Grant (1968) reported a daily maintenance requirement of 85–105 kJ for a 70–80 g starling kept in a small cage at 70–80°F. The existence energy of an 80 g bird at 75°F (23.8°c) calculated from the above equation is 117.6 kJ per day, which suggests that the equation gives a reasonably accurate estimate of starling existence energy. The daily energy requirements given in Table 7 were calculated by using the above equation to determine the existence energies at temperatures of 12.6°c and 5°c, the average daily temperatures for 23 March and 18 June respectively (as recorded at the Winchmore Irrigation Research Station, 6.5 km from the study area), and assuming that the energy requirement of a free-living starling is 1.5 times the existence energy. The day-lengths were 12 h for 23 March and 8 h for 18 June.

The calorific contents of prey determined by oxygen bomb calorimetry were 22.31 kJ per g dry weight for third-instar grass grubs and 15.23 kJ per g dry weight for earthworms. Average dry weight of third-instar grubs was 0.028 g, average moisture content being 80.9%, and the corresponding figures for earthworms were 0.100 g and 72.3%. Assuming the efficiency of utilisation of grass grubs and earthworms by starlings to be 70% (cf. Gibb 1957), the average metabolisable energy available to a starling is $0.70 \times 0.028 \times 22.31 = 0.44$ kJ per grass grub and $0.70 \times 0.100 \times 15.23 = 1.06$ kJ per earthworm. These values were used to calculate the yields given in Table 7 from the feeding rates in Table 6.

The shorter day length and lower ambient temperature in June resulted in an approximately 70% increase in the starling's hourly energy requirements from the March value. Comparison of the yield from grass grubs alone with the energy requirements for each day in Table 7 suggests that the birds could afford to reject or ignore earthworms and concentrate on grass grubs in this area in March but not in June. If 0.3–0.4 grass grubs were captured per min, the yield from grass grubs would be 7.9–10.5 kJ of metabolisable energy per h. By concentrating their feeding activity within areas where grass grubs could be obtained at rates of 0.3–0.4 or more per min, starlings would therefore be incrementing their energy intake by 25–35% or more of their minimum hourly requirement during June, assuming that other prey species were

equally abundant and available in grass grub-infested and grass grub-free areas. This appeared to be so for earthworms, although counts were not made. This suggests that energetically it is well worthwhile for starlings to continue to search for grass grubs within a localised area when feeding rate exceeds 0.3–0.4 grubs per min.

V. ESTIMATION OF STARLING NUMBERS

Methods

The total number of starling-hours spent on the study plots during the periods when grass grub larvae and adults were available to starlings was estimated. Starlings were observed with binoculars from a permanent hide at Winchmore plot 1 and from a stationary motor vehicle at the other plots. The boundaries of each plot were marked with white wooden pegs at 10-m intervals. The number of birds on a plot was counted every 5 min during observation periods of 1 to 12 h. Birds on the ground were counted, including those flying over a flock from the back to the front, which is the typical manner of progression of feeding starling flocks. To minimise the possibility of counting twice some birds in moving flocks, counts were made from the front to the back of the flock. Stationary and moving flocks containing up to 500 birds could be counted accurately in 4 min or less, judging by the repeatability of counts. If a count reached 500 before all the birds on the plot had been counted, the proportion of birds which had been counted was estimated by eye and the total number estimated to the nearest hundred. In tests in which this procedure was used to estimate the number of starlings in photographs of large flocks, the estimates were usually within 15% of the true number.

Results

Average starling counts are shown in Table 8. Winchmore plot 1 was frequently visited by flocks of tens, hundreds, and, occasionally, thousands of starlings from the nearby roost. Analysis of variance showed that average counts made at

Winchmore plot 1 on rain days (more than 0.2 mm) were significantly higher than those made on dry days in both years (P < 0.05). Average starling numbers at plot 1 for the total period were therefore calculated as weighted averages to allow for the difference between rain and dry days.

The 28-ha farmlet containing Winchmore plots 1 and 3 contained the only grass grub infestation within at least 1.6 km of the nearby starling roost. Simultaneous counts on 8 days (including 4 rain days) in a 1.2-ha grass grub-free area of irrigated pastureland situated on an adjacent property between plot 1 and the roost produced an average of only 73.1 starling-hours per ha per day, with no significant difference between rain and dry days (P > 0.10). The starlings clearly concentrated their feeding in the grass grub-infested area.

Counts made at the other plots were much lower (Table 8) and did not differ significantly between rain and dry days (P > 0.10). Winchmore plot 2 was 8 km from the high density area where plots 1 and 3 were situated and was visited by much larger numbers of starlings than the Lincoln plot. The latter plot was closed to grazing throughout the autumn and winter of 1969 and heavily stocked with ewes during the winter of 1970. Although starlings are known to prefer close-grazed pastures, numbers at Lincoln did not differ significantly between the two years (P > 0.10). No starlings were observed in 1969 at the Weka Pass plot, which was several kilometres from the nearest starling roost, although large flocks were frequently seen there during the winter of 1968. This emphasises that starlings cannot be relied upon to visit localised areas regularly unless there is a nearby source of birds from roosting or nesting sites.

Intensive starling counts were made at Winchmore plot 3 during the autumn and winter of 1970 (Table 9), either half of the day or the complete day being spent observing the plot on each day that counts were made. This plot comprised 0.25 ha of severely damaged pasture

TABLE 8 — Average starling counts during autumn and winter (March–August) (figures in parentheses are numbers of days on which counts were made)

| Plot | Year | Starling-hours per ha per day | | |
		Rain days	Dry days	Total
Winchmore 1	1969	3725.4 (8)	1229.9 (11)	1711.5 (19)
Winchmore 1	1970	5607.5 (4)	1024.2 (7)	2101.3 (11)
Winchmore 2	1969	167.7 (3)	145.4 (7)	152.1 (10)
Weka Pass	1969	0.0 (2)	0.0 (4)	0.0 (6)
Lincoln	1969	7.9 (11)	13.9 (23)	12.2 (34)
Lincoln	1970	4.4 (5)	3.8 (7)	4.1 (12)

TABLE 9 — Average starling counts at Winchmore plot 3, 1970 (numbers of days on which counts were made in parentheses)

Month	Starling hours per ha per day			
	Rain days		Dry days	
March	10090.6	(6)	5608.2	(6)
April	4544.4	(2)	1084.9	(12)
May	2175.7	(3)	1419.3	(9)
June	514.3	(2)	294.0	(7)
Total period	5937.5	(13)	1808.9	(34)

with a very high density of grass grubs. The 3.2-ha paddock containing plot 3 was closed to grazing from January until early April in 1970 and heavily stocked with ewes from then until June. Starlings did not feed in rank autumn pastures until they had been grazed down, but pasture growth was negligible in plot 3 because of the heavy grass grub infestation, allowing starlings to enter in large numbers and probe freely for grass grubs before the plot was grazed. As at plot 1, starling counts were significantly higher on rain days than on dry days ($P < 0.01$). The average starling population of plot 3 for the total period was 2915.4 starling-hours per ha per day.

Starling numbers at plot 3 declined markedly from March to June (Table 9) and a similar trend was apparent at plot 1. This was apparently a response to the marked decline in grass grub density over the same period (see Tables 13 and 14), since the adjacent roost was occupied by large numbers of starlings until mid–late July. There was no significant difference between starling counts made at plot 3 on the first half and second half of the day ($P > 0.05$), but on frosty mornings few starlings were seen before the ground had thawed, i.e., before mid–late morning.

Counts made at Lincoln (1969) and Winchmore plot 1 (1969 and 1970) in November and early December, when grass grub adults are a major item in the diet of adult and nestling starlings, revealed that starlings were present in much lower numbers than in autumn and winter. For example, at plot 1 the average numbers of starling-hours per ha per day were 16.8 in 1969 and 43.5 in 1970 (cf. Table 8). The large winter roost in this area had disbanded and most of the starlings present were resident breeders and their fledglings.

Other species — The only other bird species known to prey on grass grub larvae recorded in this study was the white-backed magpie, *Gymnorhina hypoleuca* (Gould), which was

observed in low numbers on all plots except Winchmore plot 3. Average numbers on other plots between March and August varied from 0.03 (Winchmore plot 1), to 3.5 (Weka Pass) magpie-hours per ha per day.

Other species observed searching for grass grub adults beneath pasture vegetation and surface litter at the study plots in November and December were white-backed magpies, skylarks (*Alauda arvensis* L.), house sparrows (*Passer domesticus* L.), and white-faced herons (*Ardea novaehollandiae* Latham); all were recorded in very low numbers.

Discussion

The higher starling counts on rain days than on dry days during autumn and winter at Winchmore plots 1 and 3 may have been partly due to the softer soil on rain days making grass grubs easier to obtain, and, therefore, attracting larger numbers of starlings, and partly due to the effects of overcast weather on starling dispersal. Hamilton & Gilbert (1969) found that starlings dispersing from a winter roost on overcast mornings did not travel as far from the roost, flew with less accurate orientation, and occurred in larger flocks than on clear mornings.

The average starling population during autumn and winter at Winchmore plot 3 (2915.4 starling-hours per ha per day) was considerably higher than the averages of 1700–2100 starling-hours per ha per day recorded at plot 1, which were typical of starling numbers in grass grub-infested areas of the 28-ha farmlet which contained plots 1 and 3. Higher numbers were probably attracted to plot 3 by the higher grass grub density there. The occurrence in this area of an isolated grass grub infestation close to a large starling roost resulted in an exceptionally high starling population during autumn and winter, when third-instar larvae were available. In contrast, the numbers recorded at the Lincoln plot represent a resident population of less than 2.5 starlings per ha, which is typical of most Canterbury pastureland.

Other species of birds known to prey on grass grub larvae or similar soil-dwelling larvae of other insects include the native kiwis (*Apteryx* spp.) (Watt 1971), weka (*Gallirallus australis* Sparrman) (Smith 1885), and pukeko (*Porphyrio melanotus* Temminck) (Anon. 1967; personal observations), and the introduced white-backed magpie (McIlroy 1968) and rook (*Corvus frugilegus* L.) (Oliver 1955). Grass grub adults sheltering above the soil surface during the day are exposed to predation by these species, and by insectivorous surface-feeding birds which do not probe for subterranean prey, such as the black-billed gull (*Larus bulleri* Hutton) (Myers &

Atkinson 1924), pipit (*Anthus novaeseelandiae* Gmelin) (Myers & Atkinson 1923), skylark (Oliver 1955), blackbird (*Turdus merula* L.), and song thrush (*T. philomelos* Brehm) (Myers & Atkinson 1923; Dumbleton 1942), and other passerines which are quick to take advantage of abundant insect food, e.g., the house sparrow and yellowhammer (*Emberiza citrinella* L.) (McIlroy 1968). The nocturnally active adults of *C. zealandica* and other scarabaeids are freely available to crepuscular and nocturnal predators such as the weka and pukeko (Buller 1888), magpies (McIlroy 1968), owls (Marples 1942), rats and mice (Vestjens 1970), and the hedgehog (*Erinaceus europaeus* L.) (Campbell 1973). However, it is clear from the counts and observations made during this study that, usually, all of the vertebrate predators of grass grub larvae and adults are either absent or present in only small numbers in any localised area of Canterbury pastureland infested with grass grubs. The only exception encountered in this study was the area of high starling numbers at Winchmore.

VI. PREDATION ON GRASS GRUB LARVAE

Methods

Exclusion — Starlings were excluded during autumn and winter by either metal-framed plastic netting cages 3.6 m square or wooden-framed wire netting cages 2.7 m × 1.8 m. Survival of grass grubs under the cages was compared with that in equal-sized areas of open pasture. Details of the size and number of cages, period of exclosure, and sampling times for each plot are given in Table 10. At each plot there were equal numbers of caged and uncaged areas, which were located randomly in early autumn in parts of the plot showing visible signs of grass grub damage. At Winchmore plot 1 in 1969 only half of each

3.6-m square exclosure was caged, the other half being fenced to exclude sheep but not birds. The pasture in the caged areas was mown to keep it at a similar height to the open pasture. Exclusion cages used in the measurement of pasture production are known to cause changes in temperature and humidity which can significantly affect herbage growth (Cowlishaw 1951; Williams 1951), although metal-framed, open-topped cages have no effect on temperature (Lynch 1960). Temperature measurements on the pasture surface and at a depth of 2.5 cm indicated that the exclusion cages used in this study did not significantly affect the grass grubs' physical environment.

Grass grub population densities before and after larval predation were determined by taking 15-cm spade squares (6–8 per caged and open area) at Winchmore and 10-cm diameter cores (8–10 per area) at Lincoln and Weka Pass. Grass grubs were extracted from the soil samples by the flotation and wet sieving technique of Kain & Atkinson (pers. comm.). Predation on larvae at Winchmore plot 1 in 1970 was assessed on 0.12-ha caged and open plots, which were large enough for full-scale population sampling of grass grub. A life table was constructed for the 1969–70 grass grub generation in each of these plots by sampling eggs, early and late third-instar larvae, and teneral adults. Each 0.12-ha plot was divided into six 20 m × 10 m plotlets for sampling, which was stratified random with proportional allocation. Survival of third-instar larvae was also measured in three open 0.04-ha areas with low grass grub densities adjacent to Winchmore plot 1 by sampling these areas at the same times as the 0.12-ha plots in March and July 1970.

Lateral dispersal of *C. zealandica* is slight (Fenemore 1965, 1970), but soil samples were taken from 1.0-m wide strips around the 3.6-m

TABLE 10 — Size and number of exclusion cages, period of caging, and sampling times at study plots

Plot	Year	Cage size	No. cages	Period caged	Sampling times
Winchmore 1	1969	3.6 m × 1.8 m	10	March – Aug 1969	March, July, and Nov 1969; March 1970
Winchmore 2	1969	2.7 m × 1.8 m	10	March – Aug 1969	March and Nov 1969; April 1970
Lincoln	1969	3.6 m × 3.6 m	12	April – Aug 1969	April and Aug 1969
Weka Pass	1969	3.6 m × 3.6 m	10	April – Aug 1969	April and Aug 1969
Winchmore 1	1970	120 m × 10 m	1	March – Aug 1970	Nov 1969; March, July, and Nov 1970
Winchmore 3	1970	2.7 m × 1.8 m	8	March – June 1970	March, April, and June 1970
Lincoln	1970	3.6 m × 3.6 m	12	April – Aug 1970	April and Aug 1970

square and 2.7-m × 1.8-m exclosures to check the possibility of lateral movement of grass grubs confounding the effects of exclusion. The 0.12-ha plots established at Winchmore plot 1 in 1970 were large enough to avoid possible difficulties arising from grass grub dispersal.

Experimental field populations — Experimental populations of grass grubs seeded into small field cages were used to estimate the number of third-instar grubs destroyed by starlings at Winchmore plot 3 in 1970, and to provide an independent estimate for comparison with that obtained by exclusion. Each field cage was constructed by removing a soil core 4 cm in diameter and 3 cm deep, fitting a circular piece of aluminium screen netting (seven meshes per cm) into the hole, and replacing the core. The resultant cage was 4 cm in diameter and restricted the vertical movement of a grass grub seeded into it to the top 3 cm of soil, where it was exposed to starling predation. Field cages were constructed 2–3 months before they were used to allow grass roots to grow freely through them and traces of soil disturbance to disappear. The absence of grass grubs from newly constructed field cages was ensured by either constructing them in mid December, when no larvae were present in the top 3 cm of soil (section III), or by replacing the soil core with one taken from a grass grub-free area. A wooden frame 0.9 m square containing 12 numbered positions was used to relocate field cages, which were constructed in groups or "frames" of 12, the position of each frame being marked with white, metal pegs.

Two thousand four hundred field cages were constructed in Winchmore plot 3, in 200 frames of 12, with an additional 600 cages for controls. The study period was divided into 11 time intervals. At the beginning of interval 1 a third-instar grass grub was seeded into field cage 1 in each of the 200 frames, using a 7-mm diameter cork borer. At the end of interval 1 and the beginning of interval 2, field cage 1 was removed from each frame for later examination by flotation and wet sieving and a grass grub seeded into field cage 2 in each frame, and so on. In this way an experimental population of 200 grass grubs was placed in the plot at the start of each interval. In addition, 50 grass grubs were seeded individually into field cages beneath 2.7 m × 1.8 m exclusion cages at the beginning of each interval. There were 11 time intervals of 4–13 days, 11 of the 12 positions in each frame being used.

Starlings were assumed to have removed grass grubs which disappeared from field cages. The proportion of the grubs in the top 3 cm destroyed by birds during each interval (MB) was given

by the proportion of the experimental population which disappeared minus the proportion of the controls which was not recovered. On each day that field cages were removed and fresh ones seeded, the density of grass grubs in the top 3 cm of the plot was measured by taking 200 randomly located soil cores 4.0 cm in diameter and 3.0 cm deep and extracting the grubs by hand sorting. By assuming that the density of grubs in the top 3 cm changed linearly with time from d_1 at the beginning of an interval to d_2 at the end of the interval, t days later, the average number of grass grub-days spent in the top 3 cm during the interval can be calculated as $\frac{(d_1 + d_2)}{2} t$.

If birds are assumed to remove the same proportion of grubs from the top 3 cm on each of the t days, viz., $\frac{MB}{t}$, the number destroyed by birds in the interval (NB) is given by:

$$NB = MB \frac{(d_1 + d_2)}{2}.$$

The experimental field populations gave a direct estimate of the proportion of grass grubs in the top 3 cm crushed by sheep treading. Trials in which freshly crushed third-instar grass grubs were placed in the field for known periods indicated that 100% of the remains of crushed grubs can be extracted from field cages for the first 10 days after death, with 90% recovery up to the 14th day. The number of grubs destroyed in the top 3 cm by sheep treading during an interval (NC) was therefore estimated from $NC = MC \frac{(d_1 + d_2)}{2}$ where MC is the proportion of the experimental population recovered as crushed remains (excluding the few freshly crushed grubs damaged during extraction).

The 200 grass grubs seeded in plot 3 in experimental populations had a negligible effect on the size of the natural population, which ranged from 102 to 1133 m² during the study.

Results

Exclusion — The effects of excluding starlings during autumn and winter on grass grub mortality are shown in Table 11. D was calculated from $D = D_u - D_c$, where D_u is the average difference between the initial and final densities for open areas and D_c is that for caged areas. Analysis of variance of the differences for caged and open areas was used to test whether caging significantly reduced mortality. The standard error of D was estimated by $\sqrt{2 s^2/n}$ where s^2 is the error mean square and n is the number of differences per treatment (caged and open). F-tests indicated that it was safe to assume homogeneity of the variances

of both individual samples and differences for caged and open areas.

Exclusion of starlings had a major effect on the mortality of third-instar grass grubs in the area of very high starling numbers where Winchmore plots 1 and 3 were situated. Ninety-five percent confidence intervals for the reductions in grass grub mortality caused by caging at these plots were 54.3 ± 18.9% (March–July) and 30.6 ± 26.5% (March–November) for plot 1, and 44.1 ± 15.0% (March–April) and 65.2 ± 22.6% (April–June) for plot 3. (The same caged and open areas were sampled in March, July, and November at plot 1, but fresh areas were located in April at plot 3 for resampling in June.) Exclusion of the low starling populations of the other plots did not significantly affect grass grub mortality. This confirms that the exclusion cages did not alter the physical environment sufficiently to markedly influence grass grub mortality.

At Winchmore plot 1 between July and November 1969, when starling predation had largely ceased, mortality of grass grubs was significantly greater (P < 0.05) in caged areas (29.9%) than in open areas (13.1%), partly compensating for the 54.3% increase in mortality in open areas between March and July when there was heavy starling predation. The source of the July–November mortality was not identified.

Between March and July 1969 grass grub mortalities in strips 1.0 m wide around caged and open areas at Winchmore plot 1 were 70.5% and 61.1% respectively, compared with mortalities of 11.1% within caged areas and 68.4% in open areas. The similarity of the mortalities in strips around both caged and open areas to that in the open areas suggests that significant lateral movement of grass grubs between exclusion areas and adjacent pastureland did not occur in the period March–July. The populations of 500–600 third-instar larvae per m² at plot 1 suppressed the growth of the irrigated pasture, but caused little death of plants. Under these conditions there appeared to be negligible lateral movement of grass grubs or lateral extension of pasture damage. This contrasts with the unirrigated Lincoln plot, where more than 95% of the grass grub population occurred in or within 1.0 m of discrete areas of severely damaged pasture. The proportion of the population in the 1.0-m margin of undamaged pasture around damaged areas increased from 11.7% to 28.3% from second-instar to late third-instar larvae, similar to the situation reported by Kain & Atkinson (1970). Exclusion of starlings from damaged areas at Lincoln would still have been expected to have a noticeable effect on grass grub survival if predation had been significant. Populations of more than 1000 third-instar larvae per m², as at Winchmore plot 3, caused severe

TABLE 11 — Results obtained by exclusion of starlings (D = average decrease in mortality caused by caging, expressed as a percentage of the initial population in caged and open areas combined)

Plot and period	Areas	Grass grubs per m²		D (%)
		Initial	Final	
Winchmore 1, March–July 1969	caged	602.2	534.9	54.3***
	open	559.2	176.5	
Winchmore 1, March–Nov 1969	caged	602.2	374.6	30.6*
	open	559.2	153.4	
Winchmore 2, March–Nov 1969	caged	645.0	407.5	9.5
	open	617.0	319.3	
Winchmore 3, March–April 1970	caged	1099.9	961.9	44.1***
	open	1167.2	529.4	
Winchmore 3, April–June 1970	caged	535.5	433.9	65.2***
	open	561.0	102.2	
Weka Pass, April–Aug 1969	caged	400.9	149.5	11.3
	open	417.8	120.3	
Lincoln, April–Aug 1969	caged	310.3	148.0	1.7
	open	283.7	116.2	
Lincoln April–Aug 1970	caged	79.0	38.9	3.8
	open	80.2	37.0	

  * Significant at 5% level
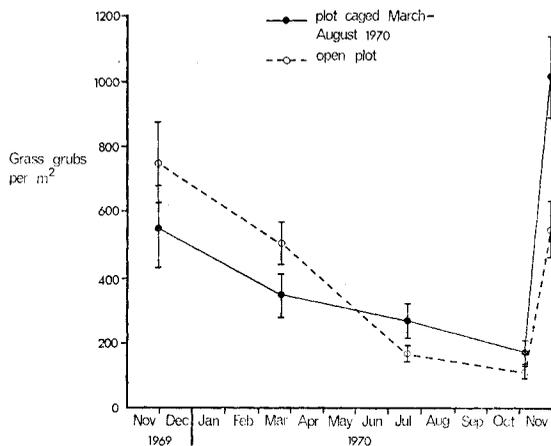*** Significant at 0.1% level

Fig. 12 — Grass grub densities in caged and open 0.12-ha plots at Winchmore. Stages sampled were eggs (late Nov 1969 and 1970), early and late third-instar larvae (March and July 1970) and teneral adults (early Nov 1970). Vertical lines represent 95% confidence intervals.

damage to irrigated pastures, with extensive death of plants and significant dispersal of grass grubs into adjacent undamaged pasture. Nevertheless, sampling in 1.0-m strips around caged and open areas at plot 3 revealed no evidence of significant lateral dispersal in the period March–April 1970, apparently because almost all the 0.25 ha of this plot was severely damaged and no exclusion areas were situated adjacent to undamaged pasture. Therefore, lateral movements of grass grub larvae during the major period of starling predation did not appear to affect significantly the results of exclusion on any of the plots.

Grass grub population trends — Resampling of Winchmore plots 1 and 2 in autumn 1970 revealed that the grass grub population in areas of plot 1 which had been caged during the previous autumn and winter had increased from 602.2 per m² in March 1969 to 841.3 per m² in March 1970, an index of population trend (see Pottinger 1967) of 139.7%, significantly greater than 100% (P < 0.01). In the open areas of plot 1 the corresponding populations of third-instar larvae per m² were 559.2 in 1969 and 473.6 in 1970, giving an index of population trend of 84.7%, significantly less than 100% (P < 0.05). At plot 2, where exclusion of starlings did not significantly affect grass grub mortality, the population of early third-instar larvae for caged and open areas combined increased from 631.1 per m² in 1969 to 1341.2 per m² in 1970, an index of population trend of 212.5%, significantly greater than 100%

(P < 0.01). These results suggest that in irrigated Winchmore pastureland grass grub populations of 550–650 third-instar larvae per m² are capable of a 1.4- to 2.1-fold increase to 850–1350 per m² in the following generation. Heavy starling predation during autumn and early winter at plot 1 apparently prevented this increase and caused a slight decline in the grass grub population to less than 500 third-instar larvae per m².

The results of life table studies of the grass grub populations in 0.12-ha plots within Winchmore plot 1 are shown in Fig. 12. The complete sample counts are given in East (1972). The major difference between the life tables for the two populations was that mortality of third-instar larvae from March to July was much higher in the open plot (66.9%) than in the caged plot (21.5%). Mortalities for the other stages were 33.2% (open) and 37.7% (caged) from eggs to early third-instar larvae and 32.1% (open) and 39.1% (caged) from late third-instar larvae to teneral adults. Fecundity was similar in the two plots. Ratios of egg densities in November 1970 to the preceding density of adult females were 11.5 (open) and 12.6 (caged). Females in the field apparently laid about half the average of 25.7 eggs per female observed in captive specimens. Dispersal of females by flight appeared to be negligible at Winchmore, over 90% of the adults trapped in flight being males. The indices of population trend (egg to egg) were 72.9% (open) and 183.9% (caged). These results are similar to those obtained with smaller exclusion areas at Winchmore: autumn populations of 350–650 third-instar larvae per m² in irrigated pastures can increase approximately 1.5 to 2.0 fold in the following generation, but heavy starling predation of third-instar larvae can prevent this and cause a slight decline.

The mortalities of third-instar larvae in three open 0.04-ha areas with low grass grub densities adjacent to Winchmore plot 1 are shown in Table 12. Although starlings had access to these areas, the mortality between March and July

TABLE 12 — Mortality of third-instar grass grubs in three open 0.04-ha plots in the Winchmore high predation area in 1970

Plot	Grass grubs/m²		% mortality
	March	July	
A	199.77	181.69	9.0
B	173.94	123.14	29.2
C	87.83	72.33	17.6

TABLE 13 — Results of experimental field population studies at Winchmore plot 3 for the period when the plot was not stocked (March–April) (d = average no. of grass grubs per m^2 in top 3 cm; MB = proportion of d removed by starlings; NB = no. destroyed per m^2 by starlings)

Interval	Length of interval (days)	Rainfall (mm)	d	MB	NB
1	7	45.7	665.83	0.33	219.72
2	7	33.0	471.49	0.28	132.02
3	7	6.8	346.16	0.22	76.15
4	4	2.0	294.37	0.09	20.60

was of the same order as that in the caged plot (21.5%), compared with 66.9% in the open plot, which had an initial population of 499.7 third-instar larvae per m². At Winchmore starlings concentrated their feeding effort on grass grubs when the local density of third-instar larvae exceeded approximately 300–380 per m² (section IV). The mortalities in Table 12 confirm that densities of less than 200 third-instar larvae per m², which cause negligible damage to irrigated pastures, are too low to attract starlings in sufficient numbers to effect significant predation.

Experimental field populations — The information obtained with experimental field populations at Winchmore plot 3 is summarised in Tables 13 and 14. Only small proportions (usually 0.04 or less) of the controls were not recovered. Standard errors were calculated for the estimated number of grass grubs destroyed during each interval.

Since NB = MB. d, where $d = \dfrac{d_1 + d_2}{2}$, the standard error of NB (s_{NB}) was calculated as the standard error of a product (Yates 1965), $s_{NB} = \sqrt{MB^2 s^2_d + d^2 s^2_{MB}}$, where s_d and s_{MB} are the standard errors of d and MB respectively. s_d is the standard error of the sum of two independent estimates, $s_d = \frac{1}{2} \sqrt{s^2_{d1} + s_{d2}}$, where s_{d1} and s_{d2} are the standard errors of d_1 and d_2, which were calculated from sample frequency distributions. s_{MB} was calculated from the large-sample binomial formula, $s_{MB} =$

$\sqrt{MB (1-MB)/200}$. The experimental populations were mixed randomly with the natural population of plot 3, and grass grub density was uniformly high almost throughout the plot. Since starlings appeared to probe randomly for grass grubs within localised areas of high grub density (section IV), it was probably safe to assume that grubs were removed at random from the top 3 cm. This was confirmed by grouping the 200 field cages seeded at the beginning of each interval into 20 groups of 10 contiguous cages, and comparing the frequency distribution of the numbers removed from these groups with the binomial distribution. Chi-squared tests revealed that the observed frequency distributions did not differ significantly from the binomial in 10 of the 11 intervals.

The standard errors calculated by these procedures ranged from 5–26% of the estimated number of grass grubs destroyed during each interval by starlings or starlings and sheep treading combined, except when mortality was very low. Total numbers of grass grubs destroyed were estimated by adding the NB and NC values in Tables 13 and 14. Standard errors could not validly be calculated for these totals, because the individual NB (and NC) estimates were not independent and each measurement of grass grub density in the top 3 cm was used to estimate d and hence NB (and NC) for two successive intervals.

TABLE 14 — Results of experimental field population studies at Winchmore plot 3 for the period when the plot was stocked (April–June) (MC and NC represent the proportion and no. per m², respectively, of grass grubs in the top 3 cm destroyed by sheep treading; other symbols as in table 13)

Interval	Length of interval (days)	Rainfall (mm)	d	MB	NB	MC	NC
5	10	0.0	280.45	0.03	8.41	0.04	11.22
6	8	0.0	262.60	0.01	2.62	0.00	0.00
7	11	41.6	224.80	0.11	24.72	0.41	92.17
8	9	0.0	173.08	0.04	6.92	0.01	1.73
9	10	20.3	137.27	0.17	23.33	0.10	13.73
10	13	24.4	107.42	0.02	2.15	0.05	5.37
11	11	56.9	61.90	0.02	1.24	0.47	29.09

Expressing the total as a percentage of the initial grass grub population gave an estimate of 39.5% for the proportion of the population destroyed by starlings in March–April, when plot 3 was not stocked. This is very similar to the estimate of 44.1 ± 15.0% obtained by exclusion for the same period.

Experimental field populations gave an estimate of 39.7% for the mortality caused by bird predation and sheep treading combined during April–June, when plot 3 was stocked, with most of the mortality (27.9%) contributed by sheep treading. In comparison, the exclusion estimate for the same period was 65.2 ± 22.6%.

Rainfall recordings in the Winchmore study area during each interval are shown in Tables 13 and 14. During intervals 1–4, when plot 3 was not stocked, rainfall was frequent and the high numbers of starlings attracted to the plot destroyed large numbers of grass grubs. The start of grazing coincided with a dry spell (intervals 5 and 6), when both MB and MC were low. Thereafter, MB and MC tended to be greater during intervals when rainfall was high and consequently the soil was soft. MC was very high during the wettest intervals (7 and 11), when the combination of heavy rain and high stocking rate (approximately 250 ewes per ha) resulted in soil puddling. Despite high rainfall during intervals 7 and 9–11, starlings caused much lower mortalities than in intervals 1–4. This was due probably to the marked decline in grass grub density in the later intervals, e.g., MB was very low during the wettest interval (11), when grass grub density in the top 3 cm was well below the range of 100–200 per m², where starlings found it profitable to concentrate on searching for grass grubs (section IV).

Mortality caused by sheep treading — Measurements of the mortality of third-instar larvae at Winchmore plot 1 in areas fenced to exclude sheep but not birds are compared with mortalities in the caged and open areas in Table 15. Initial grass grub density was similar in all areas. In

5 of the 10 fenced areas the grass was left rank (30–45 cm high), which effectively excluded starlings and resulted in a mortality similar to that in the caged areas. In the other five fenced areas the pasture was trimmed to the same height as that in the open areas (0–1 cm), giving starlings free entry to probe for grass grubs. Mortality in these areas was approximately half that in the open areas. Averages of the regular starling counts made in these two types of areas suggest that the difference in grass grub mortality did not arise from the exclusion of sheep from fenced areas, but from starlings feeding more readily in completely open than in fenced pasture. Starling predation was apparently largely responsible for the difference in mortality between caged and open areas. However, experimental field populations at plot 3 in 1970 showed that although starlings can inflict heavy mortality on high grass grub populations in the absence of stock (Table 13), sheep treading can cause mortality when the soil is soft and stocking rate high (Table 14). The apparent difference in treading mortality between plot 1 in 1969 and plot 3 in 1970 may have been a result of the different grass grub densities in the two plots, as stocking rates and grazing management were similar.

Measurements of grass grub density and soil volume weight in three 0.02- to 0.04-ha areas within a paddock on the same property as Winchmore plot 2, where starling numbers were low, are given in Table 16. After being closed to grazing for 3 months until early March the paddock was heavily stocked (137.5 ewes per ha) for 5 weeks, being grazed for 2 h per day for the first week, set-stocked for 1½ weeks, and then used as a run-off. Frequent rainfall and flood irrigation in late March kept the soil soft for most of this period and the paddock became heavily trodden. Area 1 showed no visible signs of grass grub damage, area 2 was moderately damaged, with considerable suppression of growth but little death of pasture plants, and area 3 was severely damaged, root consumption by grass grubs having destroyed most of the turf mat. The percentage

TABLE 15 — Grass grub mortalities and starling counts at Winchmore plot 1, March–July 1969

Areas	Size of areas	Average percentage reduction in grass grub density	Average starling-hours per area per day
Caged	3.6 m × 1.8 m	11.1	0.0
Fenced (grass rank)	3.6 m × 1.8 m	14.6	0.0
Fenced (grass cut)	3.6 m × 1.8 m	38.9	0.3
Open (grazed)	3.6 m × 3.6 m	68.4	1.4

TABLE 16 — Average total grass grub densities and soil volume weights in top 2.5 cm in three areas within a Winchmore paddock, before and after 5 weeks of heavy stocking during autumn

Area	Initial no. grubs/m² (March)	Volume weight (g/cm³)		Percentage increase in volume weight	Percentage of grubs damaged in final sample
		Initial	Final		
1	25.83	0.879	1.013	15.2	8.3
2	516.66	0.913	1.018	10.3	12.2
3	921.38	0.895	1.170	23.5	32.3

increase in soil volume weight after the period of heavy stocking was significantly higher in area 3 than in the other two areas ($P < 0.05$). A small number of 15-cm spade squares taken from each area after the removal of the sheep to estimate the proportion of the grubs damaged revealed that this was also significantly higher in area 3 ($P < 0.01$). The samples were stored before extraction by flotation and wet sieving and it was not possible to distinguish grubs damaged during sampling from those crushed by sheep treading, but the proportion damaged during sampling would be expected to be similar in all three areas.

Discussion

Exclusion — The high starling predation observed at Winchmore plots 1 and 3 is exceptional. The negligible predation recorded at the other plots is typical of Canterbury pastureland.

The similarity of grass grub population trends in small and large exclosures in the high predation area suggests that dispersal of grass grubs did not affect the results of exclusion. However, the significantly smaller ($P < 0.05$) increase of grass grubs from 1969 to 1970 in 3.6 m × 1.8 m caged areas of Winchmore plot 1 (1.4 fold) than in 2.7 m × 1.8 m areas at plot 2 (2.1 fold) may have resulted from random dispersal of adult females before oviposition at plot 1. It is well known that, typically, grass grub females do not fly before mating on the pasture surface, but burrow down close to the point of emergence (Kelsey 1951, 1968; Fenemore & Perrott 1970), with the result that most of the eggs are laid in the areas occupied by the previous generation, although females may fly in large numbers after they have laid most of their eggs (Kain pers comm.). Observations of females revealed that after mating they occasionally crawled several cm from their emergence sites before burrowing. This movement appeared to be random and might, therefore, have resulted in a net loss of females from the caged areas at plot 1, which were islands of high grass grub density at the time of the teneral adult sample in November,

but not from the exclosures at plot 2, where starling predation was negligible and the density of grass grub adults differed much less between caged and open areas.

Comparison of results of exclusion and experimental field populations — The close agreement between the estimates of predation mortality obtained by exclusion and experimental field populations for the period when Winchmore plot 3 was not stocked is probably fortuitous, but the similarity of the two estimates suggests that exclusion measured the absolute magnitude of predation. Exclusion of predators demonstrates directly the effect of predation on the prey population (DeBach 1958), but the difference in survival of prey between caged and uncaged areas may be less than, equal to, or greater than the number of prey consumed by predators, depending on the degree of interaction between predation and contemporaneous mortalities. If predation acts contemporaneously with one other mortality factor, using the terminology of Morris (1965), prey survival in uncaged areas (s_u) will be given by

$$s_u = 1 - (m_1 + m_2) + v m_1 m_2$$

where m_1 and m_2 are the proportions of the prey population that would be killed by predation and the contemporaneous mortality respectively, acting alone, and v is Morris's index of vulnerability. If the environment of the prey in the exclusion areas differs from that of the rest of the population in only one respect, the absence of predators, the only difference between caged and uncaged areas will be that $m_1 = 0$ in the former. Prey survival in the caged areas (s_C) will therefore be given by

$$s_C = 1 - m_2$$

and the difference in survival betwen caged and uncaged areas (D) by

$$D = s_C - s_U = m_1 - v m_1 m_2$$

D will equal only the predation mortality, m_1, if there is no interaction between m_1 and m_2 ($v = 0$) or if there is no contemporaneous mortality ($m_2 = 0$). Predators will often remove some prey individuals which would have suc-

cumbed to contemporaneous mortality in the absence of predation $(v > 0)$, in which case $D < m_1$. In the extreme case predators are able to capture only prey which would have died from other causes, $v = 1/m_2$ and $D = 0$.

If predators increase the vulnerability of prey to other mortality $(v < 0)$, $D > m_1$, i.e., exclusion will overestimate predation mortality. This situation is conceivable, e.g., Otvos (1965) reported that pine beetle parasites with short ovipositors attacked a higher proportion of the host population in areas where woodpecker feeding reduced bark thickness.

At Winchmore plot 3 exclusion may have measured the magnitude of predation, because there was either no interaction with, or a low level of, contemporaneous mortality. The latter explanation is more likely, since mortality in caged areas was low (12.1%) and captive starlings showed no marked preference for healthy grass grubs over grubs infected with bacterial (milky) and rickettsial diseases, which were the major contemporaneous mortalities.

The similarity of the estimates obtained by experimental field populations and exclusion for the period when sheep were absent from plot 3 suggests that the lower estimate obtained with experimental field populations for the period when sheep were present may have resulted from this method underestimating the mortality caused by sheep treading. Field cages did not appear to be strong enough to protect seeded grass grubs from being crushed by sheep treading, but this factor may have caused considerable mortality of grass grubs at depths greater than 3 cm; e.g., O'Connor (1956) found that soil compaction caused by stock treading extended to depths of 7–8 cm. Experimental field populations estimated sheep-treading mortality in only the top 3 cm.

Mortality caused by sheep treading — The results in Table 16 suggest that sheep treading will cause high mortality of third-instar grass grubs in heavily stocked, irrigated Winchmore pastures only when the grass grub population is large enough to destroy almost all the root system and hence reduce the resistance of the soil to compaction. It is well known that the presence of a good plant cover, turf mat, or layer of organic matter protects soil against compaction by animal treading and machines (Parker & Jenny 1945; Free et al. 1947; Taylor 1955; O'Connor 1956). Whereas populations of over 1000 third-instar grass grubs per m², as at Winchmore plot 3 (where treading caused considerable mortality — Table 14), severely damaged irrigated pasture, populations of 500–600 per m², as at plot 1

(where treading appeared to cause little mortality — Table 15), cause only moderate damage (section IX) and apparently do not weaken the strong root system of well-established irrigated pastures sufficiently to allow excessive soil compaction and crushing of grubs. This explanation is supported by measurements of soil volume weight in the top 2.5 cm of the paddocks containing plots 1 and 3 before (March) and after (June–July) periods of heavy stocking in 1970. Initial volume weights were 0.86–0.94 g per cm³. Volume weight increased by 12–16% in apparently undamaged areas with very low grass grub populations, by 18% in a moderately damaged area with a March population of 581 grubs per m², and by 35% in plot 3, where there were more than 1000 grubs per m² in March.

The combination of a severely damaging grass grub infestation and high autumn and winter stocking rate was not encountered in any of the other study plots, where exclusion of birds and stock did not affect the mortality of third-instar grass grubs.

Many of the grass grubs recovered dead in experimental populations at Winchmore plot 3 after periods of soil puddling were not crushed. These grubs may have been killed by oxygen shortage or an excess of carbon dioxide, since the decrease in gaseous diffusion which accompanies soil crust formation when puddling occurs may lead to oxygen deficiencies detrimental to plant growth (Domby & Kohnke 1956; Edmond 1958).

VII. PREDATION ON GRASS GRUB ADULTS

As noted in section V, starlings were present at the Lincoln plot and Winchmore plot 1 in much lower numbers in November and December, when grass grub adults are available, than in autumn and winter. Nevertheless, erection of nesting boxes in 1969 had increased the breeding population of starlings in the 28-ha Winchmore farmlet, where plots 1 and 3 were situated, to approximately five pairs per ha in 1970. This is far in excess of the average density in Canterbury pastureland, where typically the shortage of nesting holes limits the breeding population to densities of the order of one pair per 10–20 ha (personal observation; Coleman 1972).

A population of five pairs of starlings per ha could have an appreciable effect on populations of grass grub adults. Data obtained by other workers and summarised by Royama (1966, table 4) show that the daily food consumption (fresh weight) of a 12- to 19-day-old starling nestling is approximately half its body weight of 75 g. If grass

grub adults comprised ¾ of the diet, each nestling would consume on average 37.5 × 0.75/0.09 = 312.5 grass grubs per day, 0.09 g being the average fresh weight of a grass grub adult. Some idea of the maximum potential consumption of grass grubs by a breeding population of 5 pairs of starlings per ha can be obtained by assuming that there are 5 nestlings per brood, a 21-day nestling period, and that adult starlings consume 5 times as much as nestlings (Royama 1966), which gives 15 × 312.5 × 21/2000 = 49.2 grass grub adults destroyed per m². This represents approximately 10–50% of the teneral adult populations of 100–400 per m² recorded at Winchmore. These calculations probably considerably overestimate the magnitude of predation at Winchmore plot 1, since younger nestlings would consume considerably less than would 12- to 19-day-old nestlings. The breeding adults did not collect food entirely from within the 28 ha of pastureland where their nests were located, and Coleman (1972) found that starlings reared an average of only one or two fledglings per brood at West Melton; but these calculations suggest that dense breeding populations of starlings may consume significant proportions of grass grub adult populations.

Exclusion results

Indices of population trend in exclusion areas at Winchmore where starling predation of third-instar larvae was nil or negligible were 212.5% (plot 2), 183.9% (0.12-ha caged area within plot 1), and 139.7% (3.6-m × 1.8-m caged areas of plot 1). The breeding population of starlings at the property containing plot 2 was very low, with only a few nesting sites available around farm buildings, and none available within 1.0 km of the plot. The indices of population trend did not differ significantly (P > 0.10) between plot 2 and the caged 0.12-ha plot, despite the presence of five pairs of starlings per ha in the area of the latter plot, where starlings were excluded during autumn and winter but had free access when grass grub adults were available in spring. The lower trend index for 3.6 m × 1.8 m areas of plot 1 caged in 1969 may have arisen from dispersal of adult females, as discussed in section VI.

Discussion

The failure of starling predation on adults to significantly affect grass grub population trend in an area with a dense breeding population of starlings is apparently due to the lack of young adult female grass grubs in the birds' diet. Coleman (1972) found that adult grass grubs collected from collared starling nestlings were virtually all males and spent females. Adult females lay eggs at depths of 5–20 cm and may

therefore tend to be unavailable to starlings until after they have laid. Observations at Winchmore indicated that while considerable numbers of grass grub females which had yet to oviposit were in the top 3 cm of soil during the day, starlings obtained most of their food in the spring from on and above the soil surface, where male and spent female grass grub adults predominated.

VIII. DENSITY RELATIONSHIPS OF GRASS GRUB MORTALITIES

The mortalities of 40–60% inflicted by starlings on grass grub populations at Winchmore during autumn and winter (section VI) are of the same order as the mortalities recorded in many other field studies of bird predation on insect populations. Lack (1954, 1966) reviewed the literature on this subject and showed that birds may often take a large proportion of the available prey at times of food scarcity outside the birds' breeding seasons. Additional studies, mostly published since Lack's reviews, have shown that at times outside their breeding seasons insectivorous birds can destroy from 25% to more than 90% of a prey population (Barber 1925; Korol'kova 1963; Wall & Whitcomb 1964; Dahlsten & Herman 1965; Readshaw 1965; Baldwin 1968; Mattson et al. 1968; Sloan & Coppel 1968; Waloff 1968; Goss-Custard 1969; Hagley 1969; Black et al. 1970; Shook & Baldwin 1970; McCambridge & Knight 1972; Kamm 1973). Most of these studies presented isolated estimates of percentage predation, which reveal little about the effect of predation on the prey population. In particular, knowledge of changes in predation mortality with changes in prey population density may be useful for assessing the role of predation in population regulation (Varley & Gradwell 1970).

Methods

The density relationships of grass grub mortalities measured in exclusion studies at Winchmore plot 1 were investigated by plotting the k-values of the mortalities against the logarithms of the grass grub densities on which they acted (Varley & Gradwell 1960, 1970). To increase the number of points in the regressions the results from each individual 3.6-m × 1.8-m caged area and each 3.6-m square open area (1969), and from each 20-m × 10-m plotlet within the caged and open 0.12-ha plots (1970), were treated as replicates. This introduces a degree of approximation into the analysis, but strong density relationships should still be apparent.
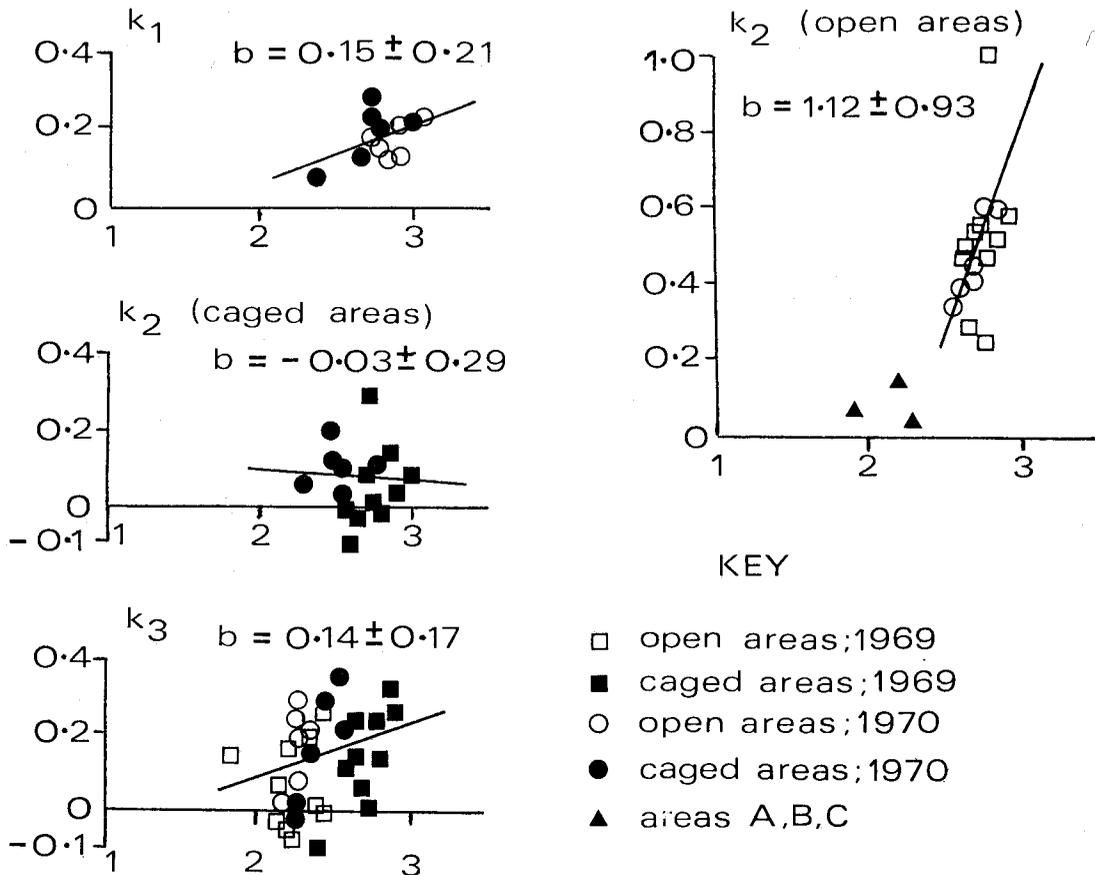
Results

k-analyses — These are shown in Fig. 13. The

Fig. 13 — Tests for density relationships of grass grub mortalities at Winchmore plot 1: plots of k-values (ordinates) against log initial densities (abscissae). b is the slope ($\pm$ 95% confidence limits). The points for areas A, B, and C (three open 0.04-ha areas adjacent to plot 1 sampled in 1970) were excluded from the regression for k_2 (open areas) (see text).

grass grub generation is split into three parts: k_1 represents mortality from eggs to third-instar larvae (late November to March), k_2 represents mortality of third-instar larvae during autumn and winter (March to July), and k_3 represents mortality from late third-instar larvae to teneral adults (July to November). The slopes of the regression lines for k_1, k_2 (caged areas), and k_3 do not differ significantly from zero (P > 0.10, P > 0.50, and P > 0.10, respectively), suggesting that these mortalities were either density independent or weakly density dependent over the observed range of densities. In contrast, k_2 in open areas where starlings had access was strongly density dependent (P < 0.05) at March third-instar densities with logarithms greater than about 2.4, i.e., populations of approximately 250 or more per m². The slope of 1.12 suggests that this mortality was overcompensatory, i.e., caused a population decline. Measurements of

k_2 in three open 0.04-ha areas (A, B, and C) with low March third-instar densities (Table 12) were of the same order as k_2 in caged areas (Fig. 13). k_2 in open areas was apparently density independent (as in caged areas) at densities below a threshold of at least 200 third-instar larvae per m², and the points for areas A, B, and C were excluded from the regression.

Observational studies at Winchmore showed that starlings increased their feeding effort in 0.25- to 0.40-ha areas of pastureland if local grass grub density increased above approximately 300–380 third-instar larvae per m², but did not respond to lower grass grub densities (section IV). k_2 in open areas at Winchmore thus appeared to be density independent at third-instar larval densities below a threshold in the approximate range 220–380 per m², but increased markedly with increases in local grass grub density above this
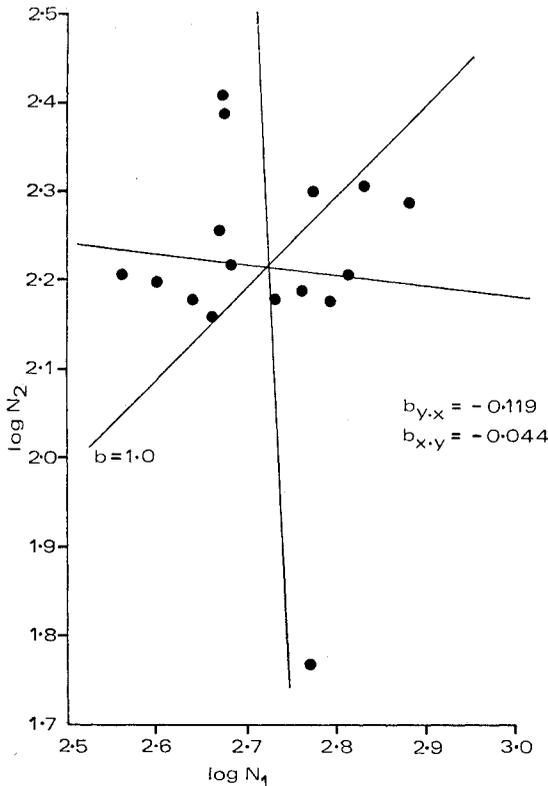
Fig. 14 — Test for density dependence of k_2 (open areas). N_1 and N_2 are the initial and final numbers of grass grubs per m^2, respectively.

threshold. The starlings showed a superproportional behavioural response (Hassell 1966) to grass grub densities above the threshold.

Test for density dependence —Density dependence can be proved by plotting the logarithm of the population density after the mortality has acted against the logarithm of the initial density; both regression coefficients ($b_{y.x}$ and $b_{x.y}$) should differ significantly from 1.0 and both lines should lie on the same side of b = 1.0 (Varley & Gradwell 1970; Luck 1971). In addition, $b_{y.x}$ and $b_{x.y}$ should both differ significantly from zero (Benson 1973). This test is carried out for k_2 (open areas) in Fig. 14. Although both slopes differ significantly from 1.0 (P < 0.001), and it could be argued that the two lines lie on the same side of b = 1.0, neither slope differs from zero (P > 0.20). Hence the density dependence in k_2 cannot be taken as proven. This test can prove but cannot disprove density dependence. It should be supported preferably by knowledge of the biological mechanisms involved, and it fails when the slope of the regression of k on log initial density approaches closely to 1.0

(Benson 1973). Since starling feeding effort increased markedly with increases in local grass grub density above the threshold, and the slope of the regression for k_2 (open areas) in Fig. 13 is close to unity, it is reasonable to conclude that this mortality was density dependent, despite the failure to prove this statistically.

Discussion

Theoretically the percentage mortality inflicted on an insect population by a vertebrate predator increases with increasing prey density up to a peak and then declines with further increases in prey density (Holling 1959a, 1965; Tinbergen & Klomp 1960). The initial increasing phase is caused by positive functional and numerical responses by the predator to prey density and results in density-dependent predation mortality which contributes to the regulation of the prey population. Satiation of the predator, the maintenance of a mixed diet (Tinbergen 1960; Holling 1965), and limitation of the predator population by some factor other than food supply set the upper limit to the number of prey consumed. Once this upper limit is reached further increases in prey density result in inversely density-dependent predation mortality, which contributes to population instability.

The density-dependent phase of bird predation on insect populations may be restricted generally to low prey densities. Since birds occur in small numbers and have limited powers of numerical increase compared with insects, it is widely held that bird predation exerts little effect on insect pest outbreaks but may be important at low or endemic levels of insect populations (Voute 1946; Morris *et al.* 1958; Gibb 1960; Buckner & Turnock 1965; Embree 1965; Miller 1966; Graham 1967). Cases where bird predation appeared to reach its peak at low prey densities and exerted no regulatory influence on prey populations at intermediate and high prey densities were observed by Mook (1963), Clark (1964), and Morris (1972). Density-dependent bird predation on insect pests at endemic levels or on insects whose populations tend to remain permanently at fairly low levels has been reported by Gibb (1958), Le Roux *et al.* (1963), Paradis & Le Roux (1965), Gage *et al.* (1970), and Furuta (1972). Inversely density-dependent bird predation during the rising phase of insect pest outbreaks, after pest populations had increased above low levels, was observed by Shilova-Krassova (1953), Readshaw (1965), and Ito *et al.* (1969).

The starling predation of grass grub larvae observed at Winchmore in this study appears to be unusual in that it caused density-dependent
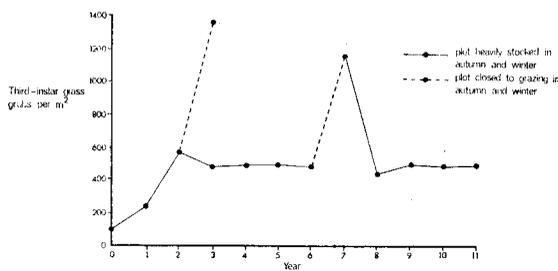
Fig. 15 — Simulated changes in grass grub population density (March) in irrigated Winchmore pastureland.

mortality over a relatively high range of prey density, from approximately 250 to at least 750 third-instar larvae per m² (Fig. 13). This range includes populations high enough to cause considerable pasture damage (section IX). Starlings did not concentrate on searching for grass grubs until grass grub density exceeded a relatively high threshold. This high threshold density was due partly to starlings being able to attack only that part of the grass grub population present in the top 3 cm of turf (40–70% at any one time), but a high threshold density may be characteristic of bird predation on concealed prey. The distance at which the predator can detect the prey affects the rate of increase in the number of prey eaten per predator as prey density increases (Holling 1965). Starlings locate individual grass grub larvae, which are subterranean and therefore concealed, by probing randomly (section IV). The threshold density above which birds found it profitable to concentrate on searching for a concealed prey which could be located only by random probing would be expected to be higher than the threshold density for an exposed prey of similar size, colour, and palatability, since the latter could be detected at a greater distance. The strong flocking action of starlings during autumn and winter and the large population in the Winchmore study area resulted in a sharp increase in predation as grass grub density increased above the threshold. Proportionately greater predation on epidemic than on endemic prey populations was also reported by Baldwin (1968), Koplin & Baldwin (1970), and Koplin (1972) for woodpeckers preying on concealed spruce beetle larvae.

Grass grub population model

A simple population model for grass grub in irrigated Winchmore pastures can be constructed from the density relationships in Fig. 13 by assuming that k_1 and k_3 are density independent and that k_2 is density independent in the absence of high numbers of starlings. Averaging observed

values gives $k_1 = 0.18$, k_2 (caged areas and areas A, B, and C) = 0.08, and $k_3 = 0.14$. By selecting an initial egg density, finding its logarithm, and using these average k-values the subsequent densities of initial (March) and late (July) third-instar larvae and teneral adults can be calculated. The size of the egg population in the next generation is obtained by assuming a 1 : 1 sex ratio and an actual fecundity of 12 eggs per female (Fig. 12). The effects of high starling predation are simulated by assuming $k_2 = 0.08$ if log N $\leqslant$ 2.40 and $k_2 = 1.12$ log N $-$ 2.54 (the regression equation for k_2 (open areas) in Fig. 13) if log N $>$ 2.40, where N is the initial number of third-instar larvae per m². k_2 is taken as 0.08 at all grass grub densities if starlings are excluded.

In using this model to simulate intergeneration changes in grass grub population density it is assumed that the density relationships of k_1, k_2, and k_3 are the same each year. Starlings appeared to exhibit the same behavioural response to local variations in grass grub density in at least the two years of this study. The slopes of the regressions of k_2 (open areas) on log initial density did not differ significantly (P $>$ 0.20) when calculated separately for 1969 and 1970 (b = 1.18 and b = 1.08, respectively). The same was true of the intercepts.

The output of this model is shown in Fig. 15, starting with a low population of 150 eggs per m² and 98 third-instar larvae per m². Since the density relationships were derived from exclusion areas, the simulated population changes are representative of areas of pastureland of 200 m² or less. The simulated population undergoes a 2.4-fold increase each year until it exceeds the threshold density for starling predation (250 per m²) in year 2, when it reaches 562 larvae per m² at the beginning of the third instar. Under the heavy stocking in the Winchmore study area high starling predation of third-instar larvae during autumn and winter begins in year 2. The simulated grass grub population declines to 468 per m² in year 3 and then stabilises at an equilibrium density of 479 per m². Over-compensatory density-dependent mortality caused by starling predation of third-instar larvae thus regulates the simulated grass grub population.

In irrigated areas of Canterbury used for fat lamb production, pasture production exceeds stock requirements during mid–late summer. This excess production was conserved in the Winchmore study area by closing parts of the farm to grazing until autumn or early winter. Starlings avoid dense, rank pasture and were effectively excluded from a paddock until it was grazed (section IV). If the pasture was left rank until

after the major period of starling predation at Winchmore (March–May), starling predation would be negligible (Table 15). If these conditions apply in year 2 the simulated population increases to 1349 per m^2 in year 3 (broken line in Fig. 15). This population density would result in the destruction of most of the pasture. The model predicts that if the plot is not grazed during autumn and early winter in any year after the equilibrium density has been attained, e.g., year 6, the population will increase to over 1100 per m^2 in the following year. Resumption of the heavy stocking–high predation treatment from year 7 on brings the simulated grass grub density back to equilibrium level by year 10.

This simple model appears to provide a realistic, broad description of grass grub population changes in irrigated Winchmore pastureland. Exclusion studies showed that populations of 400–600 third-instar larvae per m^2 normally increased by approximately 1.5 to 2.0 fold in the next generation, slightly less than the 2.4-fold increase predicted by the model, and that high starling predation entirely prevented this increase (section VI). In practice, the regulated population would be expected to fluctuate around the equilibrium density because of random variations in k_1 and k_3. Grass grub has a low fecundity, parasites are usually absent, and disease and predation are usually insignificant in Canterbury pastureland. Droughts can cause population declines, but do not affect populations of irrigated pasture. As a result grass grub populations in Canterbury typically show a steady, gradation-like increase over several years until they reach the level at which they cause severe pasture damage (Kelsey pers. comm.; Jensen 1967; East 1972). Once they have destroyed a large part of their food supply, grass grub populations are regulated by density-dependent mortality of second- and third-instar larvae caused by aggressive interactions or larval combat among larvae searching for food (Kelsey & Hoy 1950; East 1972). In the absence of high starling predation k_2 would be expected to become strongly density dependent once the density of third-instar larvae exceeded the level at which severe damage to irrigated pastures occurred, i.e., about 800–1000 per m^2. None of the points in the regression of k_2 (caged areas) on log N in Fig. 13 exceeded this level of N. The effects of larval combat are therefore omitted from the model.

Regulation of grass grub populations by starling predation at Winchmore is made possible by the low rate of increase of grass grub. Many insect pests, particularly Lepidoptera, can increase rapidly under favourable conditions, and their numbers tend to fluctuate irregularly and with wide amplitude (Ito 1959, 1961). If grass grub populations behaved in this way and were capable of a 5- to 10-fold increase in a year of favourable conditions, from below the threshold density for starling predation in one generation to severely damaging levels in the next, starlings would not have the opportunity to inflict regulatory mortality at intermediate densities.

IX. BIOLOGICAL CONTROL OF GRASS GRUB

Effects of grass grub on the production of irrigated Winchmore pastures

Methods — Pasture production was measured in irrigated areas of 80–1500 m^2 at Winchmore with low (0–150 per m^2), intermediate (400–600 per m^2), and high (800–1100 per m^2) populations of third-instar larvae in autumn (March–April). Most measurements were made within the 28-ha farmlet where starling predation was high. Autumn measurements were made in late April in paddocks which had been grazed down to cutting height (1 cm) in early–mid February and then closed to grazing for 9–12 weeks. Net pasture production over this period was measured by hand-clipping randomly located quadrats 30 cm square. Pasture production was measured in the subsequent winter (July–August), spring (October–November), and summer (January–February), while the pasture was being grazed, by the enclosure or rate-of-growth technique (Lynch 1960). Net production (regrowth) over a 2- to 4-week interval after a preliminary cut was measured beneath cages 45 cm × 30 cm. Fifteen to twenty-five percent of the fresh weight of herbage was subsampled for species analysis.

Results — The results are shown in Fig. 16, each point representing the average of 10–40 quadrats or cages (pasture production) and ten to eighty-four 15-cm spade squares (grass grub density).

Grass grub damage to irrigated Winchmore pastures is most apparent in autumn when third-instar larvae are actively feeding. Areas with fewer than 150 third-instar larvae per m^2 in autumn showed no visible signs of grass grub attack and were classed as undamaged. Local populations of 400–600 third-instar larvae per m^2 reduced total autumn pasture production by about 50% compared with undamaged areas. Perennial ryegrass (*Lolium perenne* L.), crested dogstail (*Cynosurus cristatus* L.), and clovers, which consisted largely of white clover (*Trifolium repens* L.), were affected most. Less-affected pasture components included dead material, the unsown components browntop (*Agrostis tenuis* Sibth.) and Yorkshire fog (*Holcus lanatus* L.),
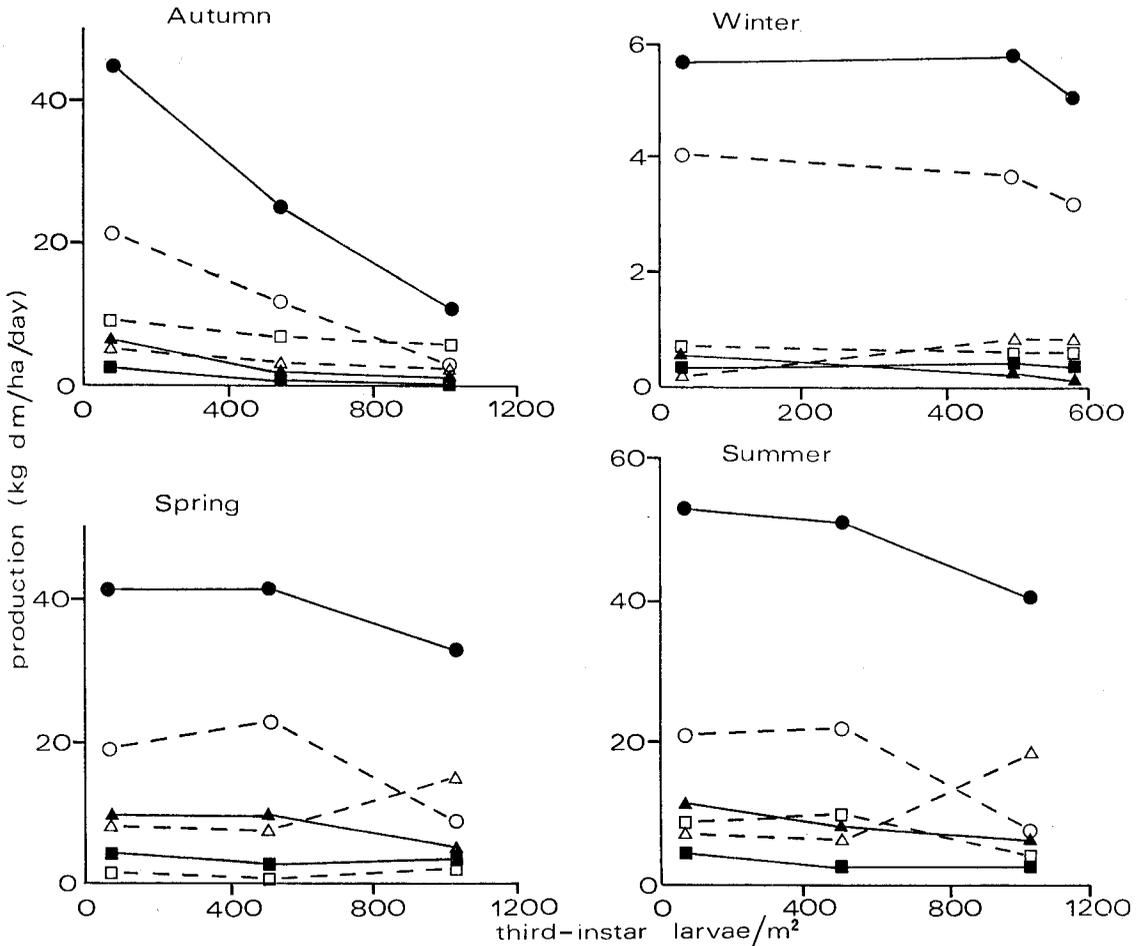
Fig. 16 — Relationships between total production of irrigated Winchmore pastures (●) and production of ryegrass, crested dogstail, and cocksfoot (○), clovers (▲), browntop and Yorkshire fog (△), miscellaneous weeds (■), and dead material (□) in autumn and the subsequent winter, spring, and summer, and the initial density of third-instar grass grubs in autumn.

miscellaneous weeds comprising mainly hairgrass (*Vulpia myuros* L.), *Poa* spp., mouse-ear chickweed (*Cerastium vulgatum* L.), and the rosette weeds *Crepis capillaris* L., *Hypochoeris radicata* L., and *Taraxacum officinale* Weber. There was little death of pasture plants at these intermediate grass grub densities and the pasture recovered during winter and early spring, after larval feeding ceased. There was no significant difference (P > 0.10) in either total production or production of individual pasture components in spring and summer between undamaged areas and areas which had intermediate grass grub densities in the previous autumn.

Grass grubs at densities of 800–1100 third-instar larvae per m² severely damaged autumn pasture. Total production was 76% less than that in undamaged areas, clovers being virtually eliminated and dead material comprising almost 50% of the total dry matter. Winter measurements of pasture production were not made in these areas. Measurements made in the following spring and summer showed that irrigated Winchmore pasture has a remarkable capacity to recover from severe autumn grass grub damage, at least under the high starling predation and high winter stocking rates where these measurements were made. This recovery was not complete, as production was about 20% less than that in undamaged areas in both spring and summer, a statistically significant reduction (P < 0.01) which was accompanied by a marked increase in the production of browntop and Yorkshire fog.

Clover production was 50–60% less than that in undamaged areas in the spring, but was not significantly less in the summer (P > 0.10). Production of ryegrass, which comprised most of the ryegrass–crested dogstail–cocksfoot (*Dactylis glomerata* L.) pasture component, remained at about 40% of that in undamaged areas in both spring and summer. Browntop and Yorkshire fog are regarded as being inferior to ryegrass. However, although they form a large part of the unsown component of high-producing New Zealand pastures, little is known about their impact on pasture or animal production (Palmer 1970; Hartley 1973).

Comparison of the pasture production measurements in Fig. 16 with those made by the rate-of-growth technique on the same soil type at the Winchmore Irrigation Research Station (Rickard & Fitzgerald 1970) shows that production in the Winchmore study area was at the level typical of good irrigated Canterbury pastures, i.e., of the order 10 000–12 000 kg dry matter per ha per year, except where it was affected by grass grub.

Discussion — The results obtained in this study show that irrigated pasture tolerates populations of 400–600 third-instar larvae per m^2, with a reduction in autumn growth and complete recovery by the following spring. In contrast, populations of 250–400 third-instar larvae per m^2 destroy unirrigated Canterbury pasture (East 1972).

These results agree with the observations of Graber *et al.* (1931), Carne & Chinnick (1957), and Chadwick (1970) that pasture plants are able to withstand and recover from the effects of root-feeding by scarabaeid larvae to a much greater extent if soil moisture and nutrients are kept at levels that promote vigorous plant growth. Similar observations have been made by several authors for pastures infested with *C. zealandica*, e.g., Dumbleton (1942) and Sears (1953). There is also evidence from pot studies that a given density of grass grub larvae has less effect on plant production if soil moisture and nutrients are in adequate supply (Radcliffe 1971). Soil moisture is the major limiting factor to pasture growth from late spring until autumn on the Canterbury Plains. Irrigation removes this restraint (Rickard & Fitzgerald 1970) and allows the pasture to tolerate much higher grass grub populations than unirrigated pasture, as noted by Kelsey & Hoy (1950).

Biological control of grass grub at Winchmore

By preventing local grass grub density from exceeding intermediate densities (400–600 third-instar larvae per m^2), high starling predation at Winchmore ensured that grass grub damage was not severe. Pasture production in infested areas was reduced by about 50% in autumn but had completely recovered by spring, a critical period in a fat lamb farming system (McMeekan 1953). An autumn survey of the 28-ha farmlet where starling predation was high revealed that 10–20% was occupied by intermediate grass grub densities, 1–2% was severely damaged, and the remainder was undamaged. Grass grub damage therefore reduced total autumn pasture production of the farmlet by no more than approximately 10% and had a negligible effect on spring production. Although the stocking rate was high for the region (19.5 ewes per ha), pasture utilisation is unlikely to have been high enough for the loss in autumn pasture production to have affected animal production.

High starling predation at Winchmore also prevented marked lateral dispersal of grass grubs. There was apparently negligible lateral dispersal of local populations of 400–600 third-instar larvae per m^2 in irrigated pastureland (section VI), probably because they did not reduce the local food supply sufficiently to be forced to disperse in search of food. The areas occupied by these intermediate grass grub densities reappeared as patches of moderate pasture damage in the same places within the farmlet each autumn, pasture growth being stunted but few plants dying. These patches did not enlarge over the 3 years of this study. In areas where grass grub density was high enough to cause severe damage to irrigated pasture there was marked dispersal of larvae into adjacent undamaged pasture (East 1972).

By preventing local grass grub density from reaching severely damaging levels at which the infestation spreads markedly from year to year, high starling predation at this farmlet has enabled successful production of export fat lambs over a 12-year period and an increase in stocking rate to 19.5 ewes per ha. This has been achieved without insecticides in a region where grass grub attack is widespread and DDT was used extensively until being banned in the late 1960s.

Components of biological control at Winchmore — Biological control of grass grub by starlings at Winchmore depended on an unusual combination of circumstances: a very large starling population, an isolated grass grub infestation, irrigation, high stocking rates, and suitable grazing management (East & Pottinger 1972).

The proximity of a large autumn and winter starling roost resulted in exceptionally high starling numbers at the grass grub-infested farmlet (section V). Surrounding properties had a history of intensive insecticide use. Starling numbers and predation would probably be much lower in the

farmlet if the roost was surrounded by an extensive area of grass grub-infested pasture. The starlings might then be more widely dispersed and tend to concentrate on the highest grass grub densities, in severely damaged pasture, rather than on intermediate grass grub densities in moderately damaged pasture. Starling predation could then cease to regulate grass grub populations at intermediate densities (cf. Readshaw 1965).

Irrigation prevents autumn droughts, which harden the soil and cause grass grubs to remain at depths where they are unavailable to starlings (section III), as well as allowing the pasture to tolerate populations of 400–600 third-instar grass grubs per m².

By heavily stocking infested pastures during autumn and winter rank pasture can be grazed short during a few weeks in autumn, enabling starlings to probe for grass grubs. Mob stocking also assists the recovery of damaged pasture by treading damaged turf, which promotes re-rooting, and by maintaining high soil fertility.

Starling predation can be manipulated by adjusting the grazing rotation each year, so that paddocks which had shown the worst signs of grass grub damage in the previous autumn are closed to grazing in January or February and heavily stocked at 250–350 ewes per ha in March and April, encouraging starlings to feed in them throughout autumn and early winter.

Integrated control — Starlings may not provide permanent biological control of grass grub at Winchmore. Since starling predation did not prevent local grass grub density from reaching 400–600 third-instar larvae per m², a large part of the farmlet may eventually be occupied by these intermediate grass grub densities. Autumn pasture production would then be significantly affected, and it may not be possible for all infested parts of the farmlet to be grazed short during the critical March–May period. In areas where starlings are excluded by rank pasture, grass grub density would increase to severely damaging levels in the following year (Fig. 15), and spring as well as autumn pasture production would begin to be affected. This situation may just have been reached during this study. The 0.25-ha area of severely damaged pasture which comprised Winchmore plot 3 in 1970 was the first such area to appear on the farmlet. The paddock containing plot 3 had remained rank until late in the critical period in 1969.

Therefore, in the long term it may be necessary to use starlings in an integrated control programme rather than relying permanently on biological control, with insecticide treatment of moderately damaged areas in paddocks which could not receive the heavy stocking–high starling predation treatment in a particular year. It would be essential to use insecticides on as small a scale as possible, since it is necessary to maintain sufficient grass grub populations to attract starlings, and the organophosphates currently recommended for grass grub control, notably fensulfothion, can cause bird deaths (Mills 1973). A small amount of severely damaged pasture could be tolerated without influencing stock production. It may be possible to use mob stocking during winter to reduce grass grub density in localised areas of severe damage, obviating or delaying the need for insecticides, since heavy stocking during periods of wet winter weather causes considerable grass grub mortality where pasture damage is severe (section VI). Other possibilities would be to change from an all-pasture farming system and introduce cultural controls (Kain & Atkinson 1970), viz., spring cultivation to destroy pupae, and sowing lucerne (*Medicago sativa* L.), which is resistant to grass grub.

The use of starlings for biological control of grass grub

The few other documented cases of bird predation exerting an economically significant effect on insect pests have also occurred in areas where there was a natural concentration of birds (Barber 1942; MacLellan 1958, 1959). Once insect pests have increased to high population densities, significant bird predation is likely to be caused only by mobile flocks (Buckner 1967), particularly if they attack localised pest populations. Suppression of localised pest outbreaks by natural concentrations of flocking birds has been recorded for predation on forest pests (Blais & Parks 1964; Mattson *et al.* 1968), locust swarms (Smith & Popov 1953; Hudleston 1958; Ashall & Ellis 1962), and for starling predation on sawfly larvae (Bruns 1960), sod webworms (Graham 1967), and grass grubs (this study). If the suppression of insect pest outbreaks by birds is generally restricted to localised outbreaks which attract large flocks, the use of starlings for biological control of grass grub may be possible only for isolated infestations close to a large concentration of starlings. Biological control at Winchmore occurred in an isolated grass grub infestation 0.8 km from a large starling roost, but predation of grass grubs was insignificant at Winchmore plot 2 (section VI) which was 8 km from the roost, well within the daily flight range of starlings.

Attempts have been made to artificially increase bird populations by erecting nesting boxes in European forests, with limited success in pre-

venting pest outbreaks in some cases (e.g., Tichy 1963; Herberg 1965; Weinzierl 1968) and none in others (e.g., Schutte 1957; Altenkirch 1963, 1968). These attempts are more likely to prevent insect pest outbreaks than to suppress pest populations which have increased to outbreak levels (Bruns 1960; Gibb 1960). Erection of nesting boxes can markedly increase local starling populations in Canterbury pastureland, where there are few natural nesting holes, and the breeding adults remain near their nesting sites throughout the year (Coleman 1972, 1974). It is unlikely, however, that local starling populations could be increased sufficiently to control grass grub infestations, unless these were very few and isolated. The average autumn and winter starling counts at Winchmore of 1700–2900 starling-hours per ha per day (section V) would be equivalent to resident populations of about 300–600 starlings per ha of grass grub-infested pasture, assuming the birds fed for 5 h per day on average. Attempts to increase local starling populations during autumn and winter by providing artificial roosting sites may not be successful, since individual roosts may be occupied each winter for many years, while apparently identical roosts closer to the starlings' feeding ground are ignored (Marples 1934).

Attempts to increase starling populations in order to combat grass grub would have to be balanced against possible detrimental affects of starlings to agriculture. Fruit consumption by starlings may be a problem (Dawson & Bull 1970), but starlings are insignificant pests of cereal crops, since grain is not a preferred food and when taken is collected mainly from the ground in stubble fields, at least in Europe (Gromadzki 1969). Fouling of buildings by roosting and nesting starlings and bird-strike hazards at airports are mainly urban problems. In extensive areas of mixed pastoral and arable farmland with no fruit growing, such as the Canterbury Plains, starlings are unlikely to have any detrimental effects on agriculture, with the possible exception of consumption of grain from winter feedlots (Coleman 1972).

In addition to high starling numbers and a localised grass grub infestation, biological control of grass grub requires irrigation (or the equivalent rainfall), high stocking rates, and adjustment of grazing management to assist starling predation. Removal of any of these factors from the system at Winchmore would probably have prevented biological control.

X. CONCLUSIONS

In most areas of Canterbury starlings occur in numbers too low to significantly affect the size of grass grub populations, but in localised areas of high starling density the birds can inflict considerable mortality (40–60%) on populations of third-instar larvae during autumn and winter. Starling predation on adults, the only other stage of the grass grub's life cycle to form a major part of the bird's diet, has a negligible effect on grass grub populations.

Starling predation of third-instar larvae can give effective biological control of isolated grass grub infestations in areas with very large starling populations, at least in combination with irrigation, high stocking rates, and grazing management which encourages starlings to feed in infested pastures. Biological control may be possible only in localised areas which have very large natural concentrations of starlings in autumn and winter.

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