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A STUDY OF WOOD-PIGEON SHOOTING: THE EXPLOITATION OF A NATURAL ANIMAL POPULATION

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INTRODUCTION

Since the late 18th century the wood-pigeon (*Columba palumbus* L.) has been recognized as a potential pest of the arable farmer, a status which was emphasized when war made it imperative to conserve home-produced food stocks (Colquhoun 1951; Murton 1965). Yet the wood-pigeon has been favoured by sportsmen, especially by those unable to shoot partridges (*Perdix perdix* L.) and pheasants (*Phasianus* sp.). As a result of studies sponsored by the Agricultural Research Council (1941–43), it was concluded that the pigeon problem could best be solved by reducing total population size, based on the false assumption that a positive correlation must exist between the incidence of real crop damage and pigeon numbers. It seemed likely that the objective of killing large numbers of pigeons could be achieved by encouraging sportsmen, and to this end, a Government subsidy was introduced in 1953 which contributed half the cost of cartridges. This bonus scheme was administered via the Divisional Pest Service of the Ministry of Agriculture.

Two main methods of shooting pigeons were adopted.

(1) 'Lone-wolf' gunners attracted the birds with artificial pigeon decoys displayed near a camouflaged hide situated by a vulnerable field crop. These sportsmen were considered the elite and their efforts effective.

(2) During February and March, after the pheasant shooting season, local gunners collaborated in roost shooting; the birds were shot as they returned to their roosting places at dusk. Such co-ordinated battue shoots were popular with Pests Officers as they could be readily organized and cartridges distributed according to the number of men participating or to the number of pigeons killed. When it was shown that battue shoots did not reduce the pigeon population below the level attained naturally and that real savings in crop damage were not achieved, Government financial support was withdrawn in early 1965 in spite of dissension from shooting advocates (Murton, Westwood & Isaacson 1964). Half-price cartridges could still be obtained through the Rabbit Clearance Societies, providing that shooting was confined to sites where pigeons caused damage. Particularly in eastern England, a shortage of rabbits (*Oryctolagus cuniculus* L.) in the mid-1960s caused farmers to relinquish their support for Rabbit Clearance Societies and to demand more action against pigeons. It was, therefore, an expediency to make it necessary to belong to a Rabbit Society before cartridges could be obtained as this helped keep societies active. However, a change in Government policy regarding financial support to the farming community led in 1969 to the abolition of Rabbit Clearance

* The study was initiated and some of the projects completed while these authors were employed by the Ministry of Agriculture, Fisheries and Food.

Societies and subsidies for cartridges. This paper examines the effects of these policy changes and demonstrates the extent to which the ubiquitous wood-pigeon is amenable to rational exploitation.

METHODS

A population study of the wood-pigeon was undertaken from 1958 to 1970 at Carlton, Cambridgeshire (1061 ha) and at nearby localities. Methods of counting the birds and of sampling their grain and clover food supply have been published (Murton *et al.* 1964).

During the first six winters battue shoots were held from late January until early March. In the following three years there was no organized shooting and only a few pigeons were killed by the gamekeeper; these can be ignored. In November 1967, some experimental shooting was begun and continued until December 1970 by Mr W. H. Edgar, one of the Ministry of Agriculture's Regional Pests staff, an ardent and highly competent pigeon shooter. It is pertinent to record that Mr Edgar rates as a top-class decoy gunner.

For the first twelve months Mr Edgar shot pigeons under our directions at sites at Carlton and nearby districts where we knew pigeons fed regularly. Either artificial pigeon decoys or dead pigeons were set-out 30 m from a shooting hide (bales of straw, camouflaged netting or cut branches) on a standard equal-sided grid at 1-m centres. From five to 200 decoys were used in separate trials. The dead pigeons were preserved by injecting them with formalin and dried either with their wings closed in a feeding posture, or with their wings open as if flying. Artificial pigeons, dead pigeons with their wings closed or dead pigeons with their wings open were used as decoys. An observer was stationed, usually in a vehicle, at a sufficient distance from the gunner not to disturb wild pigeons, but close enough to make accurate records. All wood-pigeons flying over, alone or in flocks, which passed within sighting range of the decoys were noted. The number which responded by dipping towards the decoys and/or attempting to settle, the number shot at and the number killed were recorded. Records were kept of man-hour and cartridge expenditure.

Following the termination of these experiments in September 1968, Mr Edgar was provided with all the cartridges he required and freedom of the study area and was given the task of eradicating the local wood-pigeons to the best of his ability. This phase of the work finished in October 1969 and there was relatively little shooting in the area until September 1970. Because this was an official study Mr Edgar shot pigeons as often and whenever he considered it worthwhile.

EFFECT OF SHOOTING AND FOOD STOCKS ON POPULATION SIZE

Effect of food supplies

Fig. 1 shows the changes in population size in relation to food stocks and the amount of shooting. Although some results were published in 1964 (Murton *et al.* 1964) records collected subsequently have not been published. It is, therefore, desirable to establish that the number of juveniles surviving until December depends on the amount of grain persisting on the stubbles in late autumn (Fig. 2) but that adult numbers are uninfluenced by this food supply (Fig. 3). This is because the adults can more readily turn to clover when cereals disappear. It has been shown for the first six years, that adult and juvenile numbers combined were related to grain stocks. For this purpose the 'grain index' was

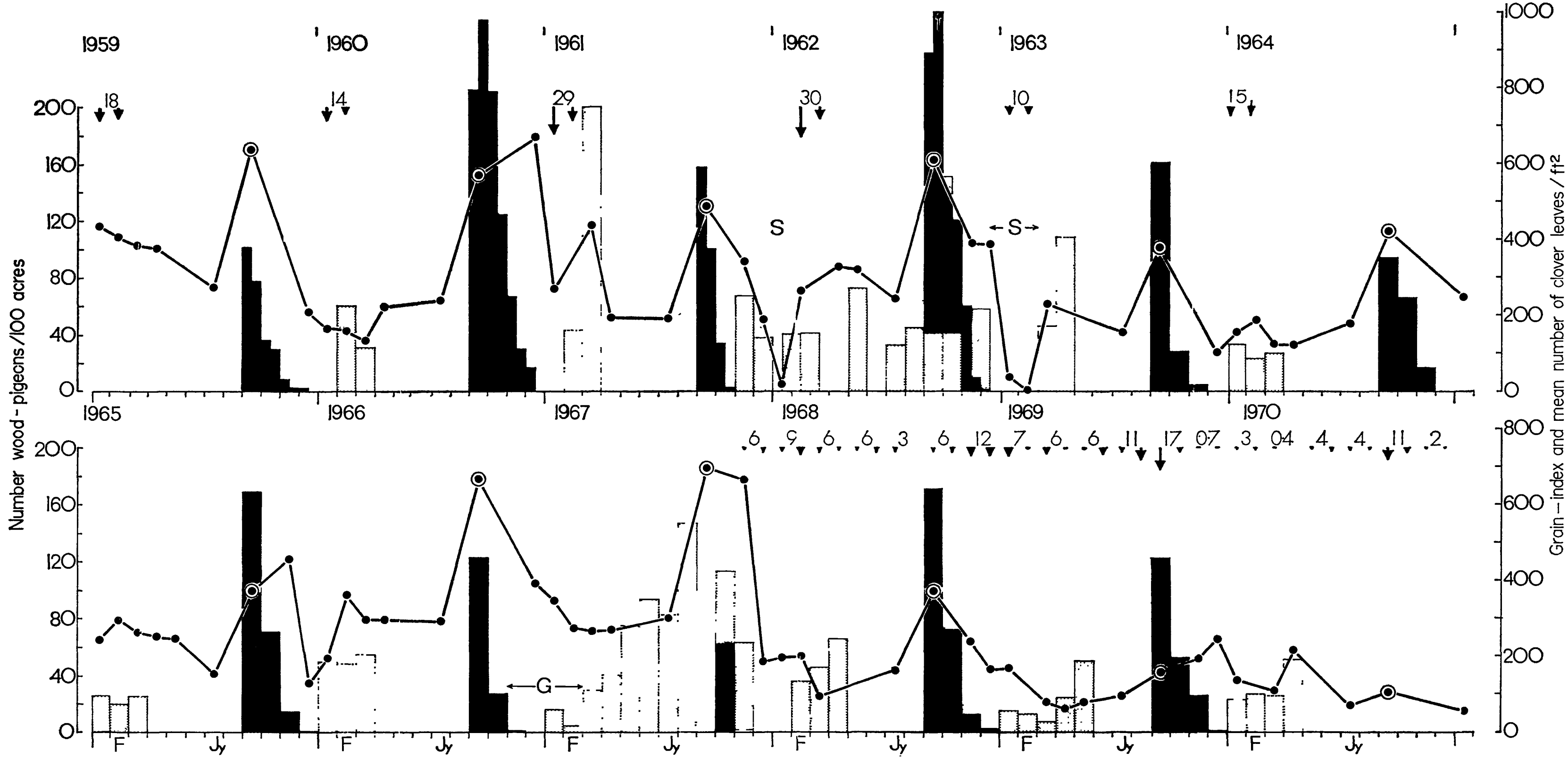

FIG. 1. Number of wood-pigeons/100 acres of a study area at Carlton, Cambridgeshire: ●, Census counts of actual birds; ◉, counts of occupied nests plus the number of chicks known to be fledged. Length of arrows indicates number of pigeons shot per month; numbers referring to the total killed/2 months. All shooting up to 1964 was of birds returning to roost and from 1967 onwards by a decoy gunner. Histograms refer to the food supply during critical seasons. The grain index is the product of the mean density of cereal grains/ft² throughout the study area and the percentage of area devoted to cereals and is shown by dark shaded histograms. The mean number of clover leaves/ft² throughout the area is depicted by light shaded histograms. During prolonged periods of snow cover (S) birds temporarily left the area to feed on nearby brassica crops. Grain (G) was abundant during winter 1966–67.

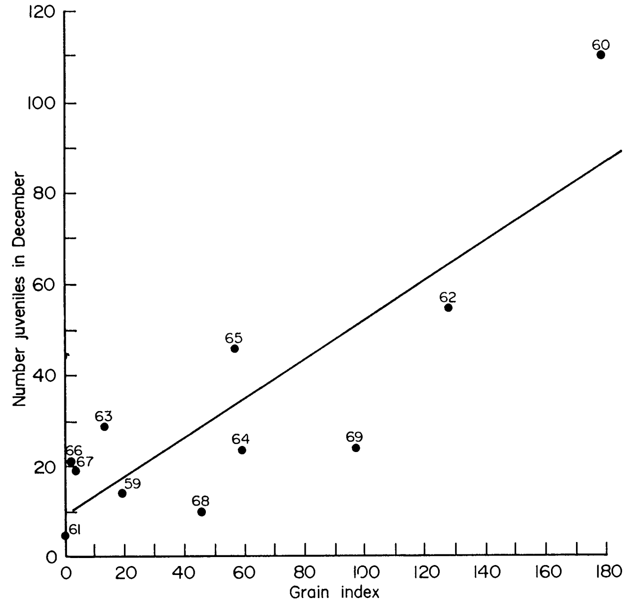

FIG. 2. Number of juvenile (< 12 months old) wood-pigeons/100 acres of the Carlton study area in early December in relation to the late November grain index (product of the mean number of cereal grains/ft^2 on all fields with grain and the percentage acreage of the study area devoted to cereals). $r_9 = 0{\cdot}852$; $P<0{\cdot}01$; $y = 8{\cdot}47+0{\cdot}43x$.

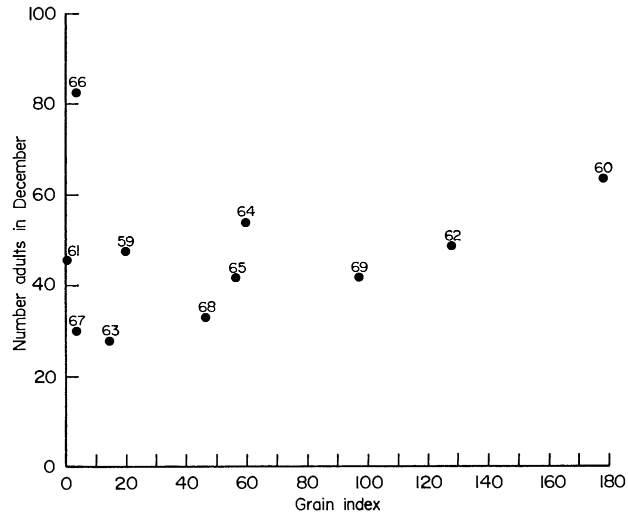

FIG. 3. Number of adult wood-pigeons/100 acres early December in relation to the late November grain index. $r_9 = 0{\cdot}215$; n.s.

calculated as the mean number cereal grains/ft^2 on all fields multiplied by the percentage of the study area under cereals. An index of total quantity was important since pigeons and other species collect cereal grain, until virtually none is left. In preliminary studies winter pigeon numbers were related to the 'clover index' which was calculated in the same way as the 'grain index'. Subsequently, it was found that the actual density of clover leaves provided a more useful measure of the winter food supply by influencing the rate at which pigeons can obtain sufficient nutrients and clover stocks become limited when a threshold density is reached (Murton, Isaacson & Westwood 1966). Moreover, the birds select from the sward and eat the most nutritive leaves; only under adverse feeding conditions do they take weed leaves (Murton, Isaacson & Westwood 1971). Unfortunately, it is not possible to identify, in the field, the leaves preferred by the pigeons and so

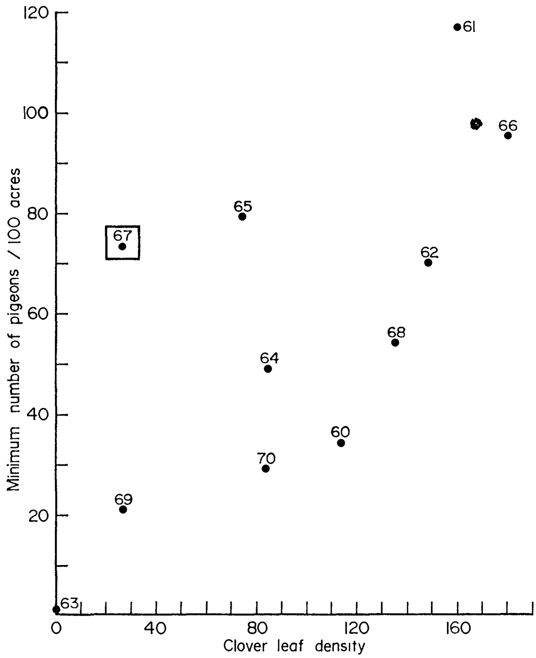

FIG. 4. Minimum number of wood-pigeons/100 acres at Carlton in winter (February–March) in relation to lowest clover leaf density recorded over the same period. $r_9 = 0{\cdot}684$; $P < 0{\cdot}02$; $y = 19{\cdot}4 + 0{\cdot}39x$. In 1967 the birds did not depend on clover due to large quantities of grain on stubbles. Omitting 1967 gives $r_8 = 0{\cdot}812$; $P = 0{\cdot}01$–$0{\cdot}001$; $y = 4{\cdot}6 + 0{\cdot}5x$.

total leaf density serves as an indication of their availability. During the study the clover acreage declined but there were winters in which leaf density was high on the remaining fields. The minimum pigeon population in late February or early March, over eleven winters, has been related to the lowest 'clover index' over the same period, confirming preliminary studies. A better correlation is obtained by using the clover leaf density, and Fig. 4 shows that the minimum total population in late February or in March was related to the lowest clover leaf density over the same period. The mortality occurring between the end of the breeding season in September and the minimum population in March can be represented as the difference between the logarithms of the two counts; negative log values indicate an increase in numbers due to immigration. The rate of juvenile loss from September until February/March shows a density-dependent relationship with the size of the post-breeding population (Fig. 5). Although the slope of the regression ($b = 1{\cdot}87 \pm 0{\cdot}49$) suggests an over-compensating density-dependent mortality factor, it is not significantly different from unity ($t_9 = 1{\cdot}77$; n.s.). Changes in adult numbers were not significantly related to density (Fig. 6), but could have been except for three years. In 1963 there was an exceptionally hard winter and the shooting mortality was responsible for the unusually high rate of loss in 1968 and 1969. Changes in adult numbers involved immigration in three out of eleven years.

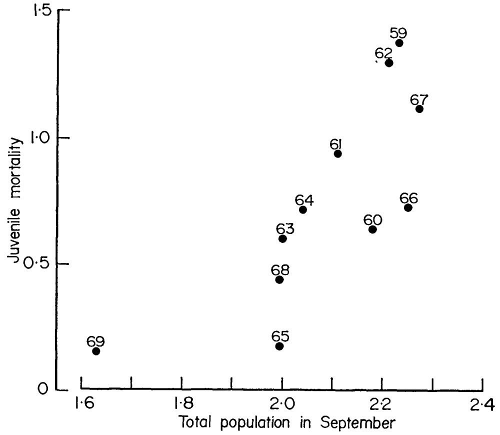

FIG. 5. Mortality of juvenile wood-pigeons in autumn and winter expressed as the difference between $\log_{10}$ population/100 acres in September and the minimum $\log_{10}$ population/100 acres in February or March. $r_9 = 0{\cdot}804$; $P < 0{\cdot}01$; $y = -3{\cdot}16 + 1{\cdot}87x$.

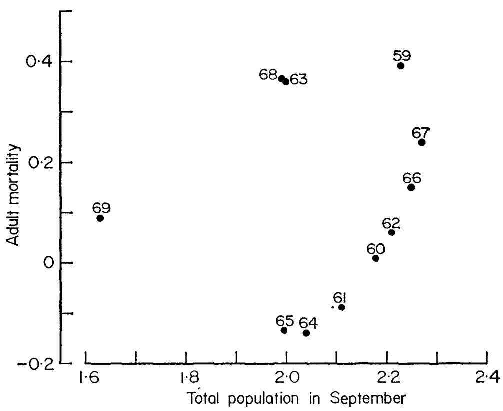

FIG. 6. Mortality of adult wood-pigeons in autumn and winter calculated as for the juveniles in Fig. 5. $r_9 = 0{\cdot}126$; n.s. Negative log values indicate that population size increased due to immigration.

Food supplies did not limit numbers between April and September for there was always more clover or cereal seed on sowings, ripening or ripe on the stalk, or wild weed seed, tree buds, and other food in excess of the amount demanded by the population; however, the ability of birds to breed in April and May was affected by woodland food supplies (Murton, Westwood & Isaacson 1974).

Effect of winter shooting at Carlton

Total populations at the start of winter (December) at Carlton are shown in Table 1 and Fig. 1. These populations, less natural losses occurring in early January, were available for shooting during the organized battue shoots during late January until early March or the experimental programmes of 1967–69. The percentages of the December totals which were shot and also the percentage change in number until April (when food stocks were not limited) which was not accounted for by shooting, are shown in Table 1. The summation of these losses and changes give the total percentage change in numbers from December until April. It is evident that the pattern of population change depended not on shooting but on other factors. The battue shoots were nullified by immigration, sometimes on a large scale. The results of the preceding section and those in Fig. 4, suggest that the amount of clover determined how many pigeons could live in the area and that if these were shot other birds moved in to fill the vacuum created.

Table 1. *Effect of shooting on changes in wood-pigeon numbers per* 100 *acres of the Carlton study area in winter*

	Total numbers in December	Total shot Dec. to Mar. (% in brackets) as minus value	Total numbers in April	Change in* numbers not due to shooting (% in brackets based on Dec. total)	Percentage change in numbers Dec. to Apr.
1958–59	117	18 (−15)	101	+2 (+1)	−14
1959–60	45	14 (−31)	59	+28 (+62)	+31
1960–61	72	29 (−40)	52	+9 (+12)	−28
1961–62	50	30 (−60)	88	+68 (+136)	+76
1962–63	104	9 (−9)	61	−34 (−32)	−41
1963–64	41	15 (−37)	32	+6 (+15)	−22
1964–65	79	0 (0)	68	−11 (−14)	−14
1965–66	52	0 (0)	79	+27 (+52)	+52
1966–67	104	0 (0)	72	−32 (−31)	−31
1967–68	52	19 (−37)	25	−8 (−15)	−52
1968–69	46	18 (−39)	21	−7 (−15)	−54
1969–70	66	3 (−5)	57	−6 (−9)	−14

* Out of 117 pigeons alive in December 1958, eighteen (15%) were shot, theoretically leaving ninety-nine. In April there were 101 birds so that two pigeons (1% of 117) must have moved into the area. Thus from 117 birds, −15% were shot, 1% were immigrants, hence the total population change between December and April was −14%.

The total percentage population change (y) was not correlated with the percentage of birds shot ($r_{10} = -0{\cdot}159$; n.s.) but was correlated with the percentage change in numbers not due to shooting ($r_{10} = 0{\cdot}901$; $P<0{\cdot}001$; $y = -19{\cdot}13+0{\cdot}81x$).

Immigration during winter probably involved surplus birds from nearby areas which would otherwise have died of food shortage. It was noticeable in the winter of 1964–65, following the abolition of the Government subsidy for battue shooting, that letters to the sporting journals expressed the presence of abnormally large numbers of dead wood-pigeons on roadside verges and the countryside. Presumably before 1964, many birds which might have died from food shortage or from other causes were being shot. This is substantiated from recoveries of ringed wood-pigeons marked under the British Trust for Ornithology scheme. Of 189 pigeons recovered during January–March 1958–64, 75% were shot. The bulk of the remaining 25% were found dead, while some birds died from injury, drowning, being killed by a cat and other miscellaneous causes. These records include a higher than average number in the found-dead category in consequence of exceptional mortality which occurred in the hard winter of 1962–63. From the same months in 1965–68, 241 pigeons were recovered of which 40% were in the found dead and miscellaneous category (60% were shot) (χ^2_1, = 9·91; $P<0{\cdot}01$).

Local movements also occurred during periods of snow as the birds could find uncovered fields of brassicae just outside the immediate census area. Immigration in May involved mostly juveniles which had migrated relatively long distances during the winter; a small proportion of the British population moves to France in early November and survivors return in April or May (Murton & Ridpath 1962; Murton, Westwood & Isaacson, unpublished). It is possible that the opportunity for long-distant migrants to return to the study area has increased since the abolition of intensive winter shooting. It is evident from Fig. 1 that the abolition of winter shooting did not lead to an increase in the local wood-pigeon population.

The shooting experiments November 1967 *to October* 1969 *at Carlton*

Clover density was exceptionally low during January–March 1969 (Fig. 4) and explains why the July breeding population was also low; the breeding population in 1970 and 1971 remained low and while leaf density was also fairly low in 1970 (Fig. 4), it was not measured in 1971. But since shooting was discontinued in 1971 it did not explain the failure of the pigeon population to increase. In September 1967, there were 186 birds/100 acres (40·5 ha) following breeding (Fig. 1) of which 142 (76%) had vanished by July 1968. Thirty birds (21% of the 142) were shot over this period. Similarly of ninety-nine birds alive in September 1968, seventy-three (74%) were lost by the following July 1969 and shooting accounted for 55% (forty birds) of these: of the mortality occurring during the winter (the population declined from forty-six in January to twenty-one in April, Fig. 1) 72% was caused by shooting. There were forty-three birds/100 acres in September 1969 of which twenty-five (58%) were lost by the following July. During the same period twenty-seven pigeons were shot/100 acres. The exceptional adult mortality affecting the 1968–69 and 1969–70 cohorts (Fig. 6), suggests that very intensive shooting caused excessive mortality in years when population size was already low (see also Fig. 1), but only in 1968–69 was the shooter trying to eradicate pigeons. Although the total amount of late summer, autumn and winter mortality of adults was apparently increased by shooting, there is no clear indication that the size of the subsequent breeding population was reduced (Fig. 1).

It might be argued that the shooting effort in 1967–68 could have been increased had not experiments been in progress. Even so, more birds were shot per hour in 1967–68 than in 1968–69 (cf. Tables 2 and 4), when the shooter was attempting to reduce numbers. If the shooting which was done after July 1969 is ignored, on the basis that a new population was now at risk following breeding, it can be calculated from the results shown in Table 2, that in 1968–69 it required about ten man-hours and nearly seventy cartridges to kill forty birds/100 acres. Table 2 gives the returns for the whole study area of 2647 acres (1061 ha) and these must be converted to the proportionate costing per 100 acres. Thus excluding travelling time and allowing a wage of £0.5/hour and a retail price of 5p/cartridge, it cost over £0.24 to kill each pigeon.

More pigeons are at risk immediately after the breeding season for population size is at first high and then declines (Fig. 1). Yet there was no consistent seasonal variation in the time required to shoot each bird nor in the expenditure of cartridges (Table 2). This

Table 2. *Number of pigeons shot and cartridges used by a decoy gunner at Carlton and other sites*

	Number pigeons shot	Man-hours expended		Cartridges /bird	Man-hours /bird
Carlton*					
Sept. 1968	78	20·5		1·7	0·26
Oct.	79	29·0		1·7	0·37
Nov.	168	46·8		2·1	0·28
Dec.	165	46·0		1·8	0·28
Jan. 1969	149	33·8		1·9	0·23
Feb.	30	7·0		1·6	0·23
Mar.	141	7·5		1·4	0·05
Apr.	33	7·0		1·7	0·21
May	23	11·0		1·4	0·48
June	140	30·5		1·5	0·22
July	72	22·0		1·6	0·31
Aug.	203	41·5		1·8	0·20
Sept.	365	86·3		1·7	0·24
Oct.	66	11·0		1·6	0·17
Total	1712	399·9	Mean	1·7	0·23
Carlton†	29	10·5		2·8	0·39
Vale of Evesham‡					
Roost	45	16·3		1·6	0·37
Decoying on clover fields	165	74·8	}	2·0	0·45
Decoying on cabbage fields	597	377			0·63
Walking round fields as in rough shooting	21	36		2·3	1·72

* Decoy shooting according to experiments detailed in text.
† Battue shooting by local guns at Carlton in 1969.
‡ By members of the West Midland Wood-pigeon Club (data from Murton & Jones 1973).

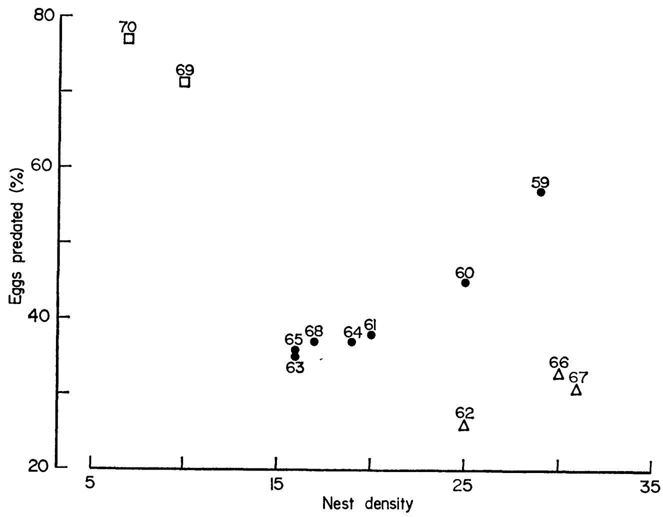

FIG. 7. Percentage of wood-pigeon eggs taken by predators throughout the breeding season in relation to the density of occupied nests/acre. Many adults were shot in 1969 and 1970 (□) during an experimental programme, while in 1962, 1966 and 1967 (△) jays and other predators were intensively slaughtered. In the remaining seasons conditions stayed constant and for these: $r_s = 0{\cdot}957$; $P < 0{\cdot}001$; $y = 9{\cdot}8 + 1{\cdot}5x$.

suggests that there was a limitation in the shooting technique. If the gunner was sited in a favourable place and pigeons were attracted to his decoys he enjoyed a successful session. But if after waiting a reasonable time no birds appeared the site was abandoned. In this way, the shooter tended to bias his prospects towards success. Table 2 gives comparative figures for the man-hour expenditure required to shoot pigeons in some other situations studied, these data representing the ability of average to good pigeon shooters.

During the main breeding season from July to September 1968, 154 pigeons were shot in the study area; 640 were killed in the same period in 1969 and 318 in 1970. This represents 14%, 96% and 61% respectively, of the adult breeding population in July. Shooting seems to have had no adverse effect in 1968, but in 1969 and 1970 the breeding success of the birds was seriously reduced (Fig. 7). Egg predation in Carlton wood was mostly from jays (*Garrulus glandarius* L.) who gain access to the eggs when the nests are left unguarded. Egg predation increases with the density of breeding pairs (see Fig. 7) and in 1969 and 1970 a low rate of predation should have been predicted. But the shooting of parent birds produced unguarded nests and the eggs were soon removed. In 1962, a new game-keeper was appointed and for one season he intensively killed predatory birds but this enthusiasm waned in the following year (see Lack 1966, p. 181). In 1966 and 1967 another game-keeper killed predators in Carlton wood and egg predation was lower than expected. An attempt was made to quantify these campaigns and occasionally the keeper revealed the number of corvids he had shot. But dead birds in the woods and on gibbets were also noted and it was evident that his records were not reliable. Birds of prey were also killed in the supposed interests of game preservation.

THE EFFECT OF USING DECOYS

For a given number of decoys the proportion of passing pigeons which respond by dipping in flight or attempting to alight declines as their flock size increases (Murton 1973). Thus single birds respond more readily to a given number of decoys than individuals in a flock of fifty. Increasing the number of decoys can increase the response of pigeons in the larger passing flocks but there are limitations (see below). Records combining the observations made when different numbers of decoys (1–200 dead pigeons with wings open or with wings closed) were used (Fig. 8), show how a smaller proportion of the flock responded as the size of the passing flock increased. As implied above a response is recognized as any deviation from the direct flight-path which could be expected in the absence of a decoy. The probability of shooting a bird which circles and attempts to settle with the decoys is obviously greater than that of shooting one which only dips in flight.

It is convenient to pool all degrees of response because defining categories is difficult, and to assume that the number of pigeons potentially at risk of being shot is a constant proportion of the total responding. Use of a double-barrelled twelve-bore shot-gun restricts the number of pigeons which can be shot to two, irrespective of the number responding at any time. Even so, the birds are only infrequently in a suitable position for long enough for the right and left barrels to be fired in quick succession at different birds, and it is more realistic to consider a maximum potential of about one bird per flock. Fig. 8 shows that if single birds were flying within the decoy area, 45% responded and of these 66% were shot, that is, 30% of all pigeons coming within range of the decoys were killed. When flocks of four were involved, 32% of the birds responded of which 25% were killed, representing only 8% of the pigeons potentially at risk. It is evident why shooters prefer situations where pigeons constantly arrive in small flocks.

The effect of varying the number of decoys on passing single pigeons, larger flocks being ignored (Table 3), avoids bias if social interaction leads to flock cohesion and group responses. Increase in the number of decoys from five to twenty-five resulted in an increase in the percentage of passing single birds which responded and this enabled a higher proportion to be shot. It made no difference to the proportion actually shot whether the decoys had closed or open wings. With more decoys there was no significant increase in the proportion of birds responding and there may even have been a decrease.

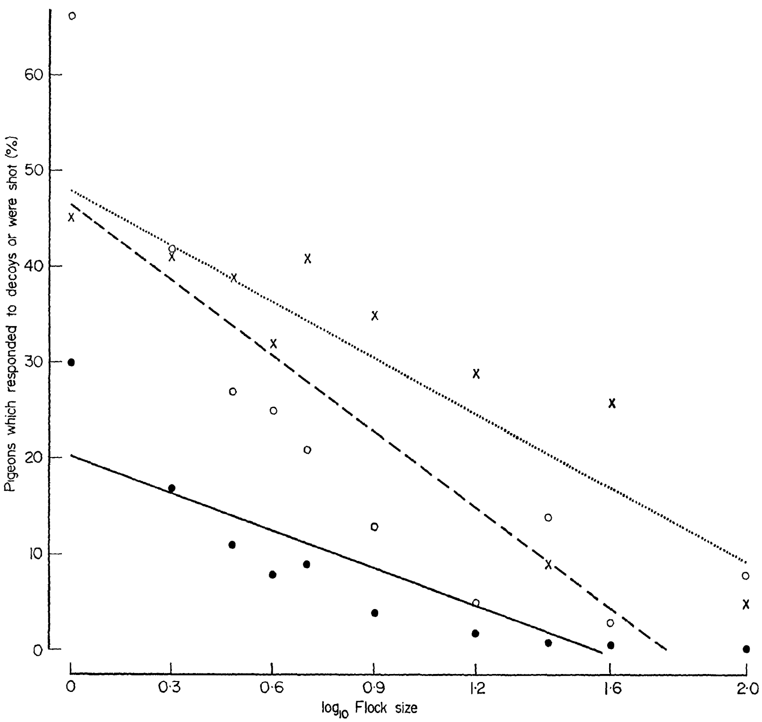

FIG. 8. Percentage of passing wood-pigeons which responded to dead pigeon decoys and were shot (records combined for experiments involving 5–200 decoys) in relation to $\log_{10}$ number of birds/flock. ×, Percentage of passing pigeons which responded by dipping or circling over the decoys or by trying to alight. $r_8 = -0{\cdot}891$; $P<0{\cdot}001$; $y = 48{\cdot}0-19{\cdot}3x$. ○, Percentage of responding birds which were shot $r_8 = -0{\cdot}848$; $P<0{\cdot}01$; $y = 46{\cdot}5-26{\cdot}2x$. ●, Percentage of birds at risk, that is, all those passing, that were shot. $r_8 = -0{\cdot}865$; $P<0{\cdot}01$; $y = 20{\cdot}2-12{\cdot}9x$.

There were indications that individual pigeons were more attracted to medium numbers of decoys (which they presumably interpreted as feeding flocks) than to small numbers but they may have been repelled by very large flocks. That this was the case is shown by the response of passing pigeons in flocks, ranging in size from one to ten birds (Table 3, Fig. 9). A logarithmic relationship existed such that with five decoys, 7% of pigeons at risk were shot, 11% with ten decoys, 14% with twenty decoys, 19% with forty decoys and 23% (the maximum) with eighty decoys (Fig. 9). It is known from other studies in which no attempts were made to shoot the birds that wood-pigeons would land next to decoys with closed wings, whereas in the presence of many open-winged decoys, live pigeons

Table 3. *Response of single wood-pigeons to decoys and percentage which were shot according to number of decoys employed (data in parentheses refer to records when flocks of one to ten pigeons were at risk)*

Number of decoys used	Number wood-pigeons passing which were at risk	Percentage of passing birds which: responded to the decoys	were shot	Number of pigeons shot which had not responded to the decoys
5 WC*	17 (53)	29 (38)	12 (9)	0 (0)
15 WC	131 (760)	34 (31)	23 (10)	13 (28)
15 WC	76 (309)	50 (36)	25 (14)	3 (6)
25 WC	75 (300)	55 (43)	44 (17)	3 (6)
25 WO	49 (334)	65 (47)	43 (14)	2 (2)
40 WC	166 (776)	53 (60)	35 (18)	4 (8)
40 WO	92 (339)	48 (46)	33 (16)	4 (4)
80 WC	43 (199)	53 (51)	51 (28)	3 (4)
80 WO	22 (185)	55 (23)	50 (10)	1 (3)
100 WC	19 (116)	32 (35)	32 (13)	2 (2)
130 WC	30 (52)	63 (46)	40 (27)	0 (0)
200 WC	133 (489)	47 (40)	29 (16)	4 (8)
200 WO	23 (139)	35 (16)	17 (7)	0 (1)
15 A	169 (562)	31 (21)	20 (8)	11 (15)
40 A	95 (544)	44 (29)	19 (7)	6 (12)

* WC, dead wood-pigeons with wings closed; WO, dead wood-pigeons with wings open; A, artificial wood-pigeons.

which had initially responded would shy away and not attempt to settle (Murton 1973). Presumably decoys with closed wings simulate pigeons feeding in a safe site; small numbers with open wings perhaps give the impression of the short flights made by feeding birds, but large numbers in flight probably signal danger.

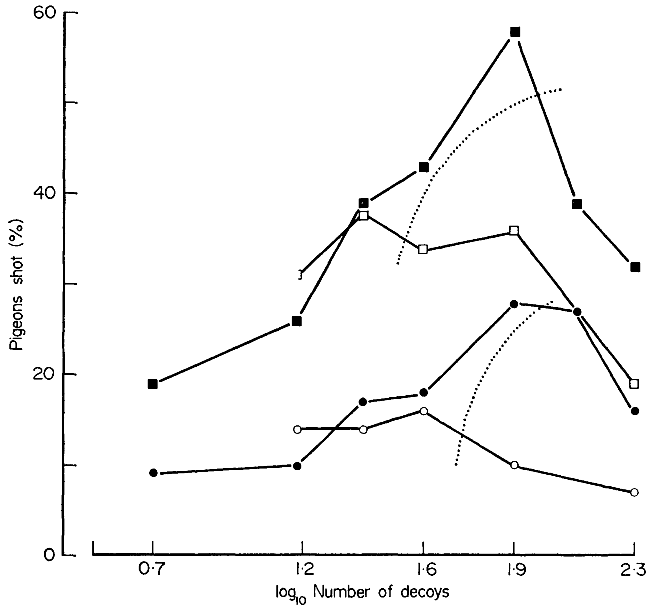

FIG. 9. Proportion of wood-pigeons which were shot in relation to $\log_{10}$ number of decoys (dead pigeons) used: solid symbols, decoys with closed wings; open symbols, decoys with open wings. Circles, percentage of passing pigeons killed; squares, total birds shot as percentage of number of passing flocks. Regressions calculated for the straight-line portions of the response graph and omit the points demarcated by the dotted lines. There is no difference in the response elicited by open- or closed-wing decoys and so these results are combined. Pigeons shot as a percentage of number of flocks at risk (squares): $r_5 = 0{\cdot}971$; $P<0{\cdot}001$; $y = -7{\cdot}4+32{\cdot}7x$. Pigeons shot as a percentage of total number of birds at risk (circles): $r_6 = 0{\cdot}877$; $P<0{\cdot}01$; $y = -3{\cdot}8+14{\cdot}3x$.

Artificial decoys produced a poorer response from the passing flocks than dead pigeons (Table 3). Comparing fifteen dead pigeons and fifteen artificial decoys shows that the latter resulted in 13% fewer pigeons being shot, and 46% fewer when forty decoys were used (Table 4).

In addition to the birds shot which responded to decoys, others were shot which passed by when the shooter was in his hide and would have been killed even if no decoys had been used. In the case when single birds were passing, an additional 11% were shot which had not responded to decoys and in flock sizes of one to ten birds combined, an additional 5% were shot (Table 3).

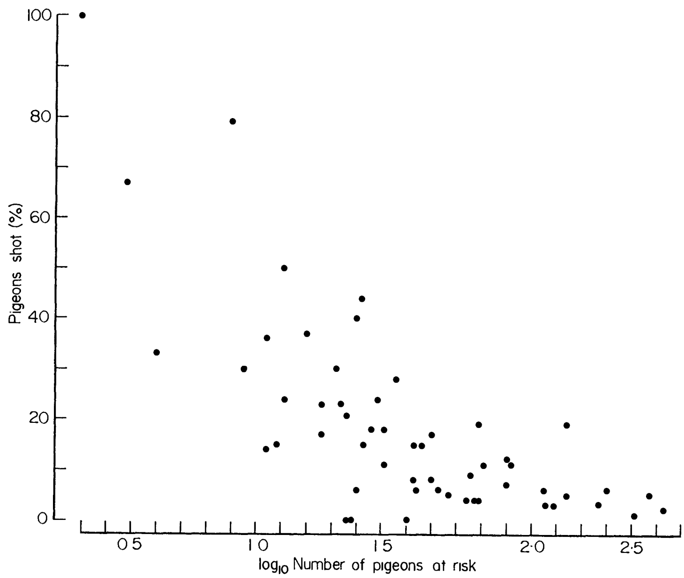

FIG. 10. Percentage of pigeons shot in relation to the $\log_{10}$ number passing within range of decoys/hour. Records combined for situations when fifteen or forty dead pigeon decoys with open or closed wings were used. $r_{53} = -0{\cdot}724$; $P<0{\cdot}001$; $y = 63{\cdot}5-28{\cdot}1x$.

Sometimes flocks containing more than ten pigeons came in range of the decoys but although the total numbers of birds at risk was large the actual number of flocks was small. Since at most two birds could be shot per flock the sampling errors were large. Table 4 summarizes data dollected when fifteen, forty or 200 decoys were used. The response and shooting rates when dead pigeons with closed wings were used increased and declined as discussed above. Fifteen dead birds with open wings were more attractive to passing birds than fifteen dead birds with closed wings, but when forty decoys were used the response pattern was reversed. Artificial decoys of the kind mostly used by sportsmen were generally less effective than dead pigeons indicating a considerable visual acuity and ability to discriminate subtle cues by the pigeons flying overhead.

The number of pigeons killed per hour was positively correlated with the proportion responding to decoys and the proportion shot but sampling errors masked the relationship. Thus the number of birds and flocks passing per hour varied on different days so that conditions were not absolutely constant for all experimental situations. The data obtained during all separate shooting sessions involving fifteen or forty dead pigeons with wings open or closed are converted to the $\log_{10}$ number of birds passing per hour and the percentage of these which was shot (Fig. 10). The more birds passing per hour

Table 4. *Percentage of passing wood-pigeons, irrespective of flock size, which were shot according to the number of decoys used*, 1967–68

	Total time (h)	Total birds at risk	Mean flock size	Percentage responding to decoys	Percentage shot of birds at risk	Percentage shot of birds responding	Percentage shot of those shot at	Number birds passing per hour	Average time to kill one pigeon (h)
15 WC*	20·9	2296	6·7	19	5	28	74	110	0·17
15 WO	12·4	911	4·4	28	7	25	63	73	0·19
15 A	20·5	1088	3·7	18	6	34	73	53	0·31
40 WC	27·0	1220	3·7	56	12	22	66	45	0·18
40 WO	11·2	526	3·2	29	12	41	64	47	0·18
40 A	7·9	869	5·3	22	5	22	49	110	0·19
200 WC	15·3	617	2·5	36	17	47	75	40	0·15

* WC = dead wood-pigeons with closed wings; WO = dead wood-pigeons with open wings; A, artificial decoys. The differences in response rate between 15 WC and 15 WO ($\chi^2 = 31{\cdot}27$; $P < 0{\cdot}001$), and between 40 WC and 40 WO, are significant ($\chi^2 = 106{\cdot}5$; $P < 0{\cdot}001$).

the lower the percentage which was shot. This inverse density-dependence obviously resulted from the fact that the shooter could have only two shots before reloading. But even if he had used a repeating gun there would have been a scaring effect from the first explosion causing the remaining birds to veer away. As might be predicted there was a poor correlation between the number of birds shot when expressed as a percentage of the total flocks passing per hour and regressed on the number of flocks passing per hour ($r_{53} = -0{\cdot}272$; $P = 0{\cdot}05$).

The time of day made little difference to the effectiveness of decoy shooting between 10.00 and 16.00 hours (Table 5). It appears, however, that pigeons did decoy less well before 10.00 hours and after 16.00 hours and shooting became less worthwhile in consequence. Early in the morning pigeons leave their roosts and depart on direct flight lines to feeding grounds which they have used the day before and they are not easily distracted. Similarly, in the evening the birds are motivated to get back to the roost.

Table 5. *Effect of time of day on efficiency of decoy shooting*

	Total no. birds passing	Number birds passing/h	Percentage passing birds responding to decoys	Percentage birds at risk which were shot	Average time (h) to kill one pigeon
Before 10.00 hours	758	84	12	5	0·23
10.00–12.00 hours	4718	78	28	7	0·18
12.00–14.00 hours	3046	66	27	11	0·14
14.00–16.00 hours	2624	61	30	9	0·19
After 16.00 hours	172	43	24	10	0·22

COMPARISON OF SHOOTING WITH OTHER METHODS OF KILLING PIGEONS AT CARLTON

Baits treated with alpha-chloralase as a stupefacient were used at Carlton to catch woodpigeons for examination and in marking and release; over 3300 pigeons were captured in this way. Baits were mostly laid on feeding grounds where good captures could be expected and in general poor feeding places were avoided. Yet it is known that a lower proportion of juveniles is captured if baits are laid on fields where clover density is low and the mean weight of both adults and juveniles is lower than for birds caught on fields of high leaf density (Murton, Isaacson & Westwood 1971).

Comparable shot or stupefied samples for several years are combined in Fig. 11 to show how the estimated proportion of juveniles in the population varied seasonally according to the method of capture. Immediately after breeding neither method adequately sampled young birds as they remained in the woods and only came to consort with adults in the fields later in the autumn. It is possible that, compared with stupefying baits, shooting was biased towards the capture of inexperienced juveniles up until December. But the number of birds caught with baits was relatively small until this time. Food supplies had not reached a critically low level in January (Fig. 1) and on average the proportion of juvenile birds in shot and stupefied samples differed by only 7%, the shot samples containing more juveniles. The situation was reversed in February and stupefied samples contained 10% more young ($\chi^2_2 = 206{\cdot}1$; $P<0{\cdot}001$). Clover stocks were usually at a minimum in February or March and young birds were concentrated on the better feeding grounds, which is where most trials with stupefying baits were conducted. Food supplies improved after March and differences depending on the method of capture were reduced.

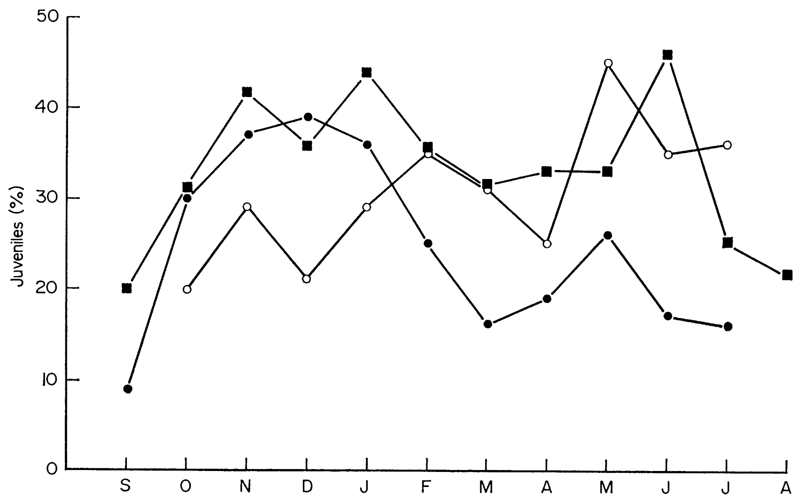

FIG. 11. Percentage of juvenile (<12 months old) wood-pigeons in shot or stupefied samples in monthly collections. ●, shot at Carlton during 1958–70; ○, caught with stupefying bait at Carlton during 1958–70; ■, ringed wood-pigeons which were shot and reported under the British Trust for Ornithology scheme during 1911–70.

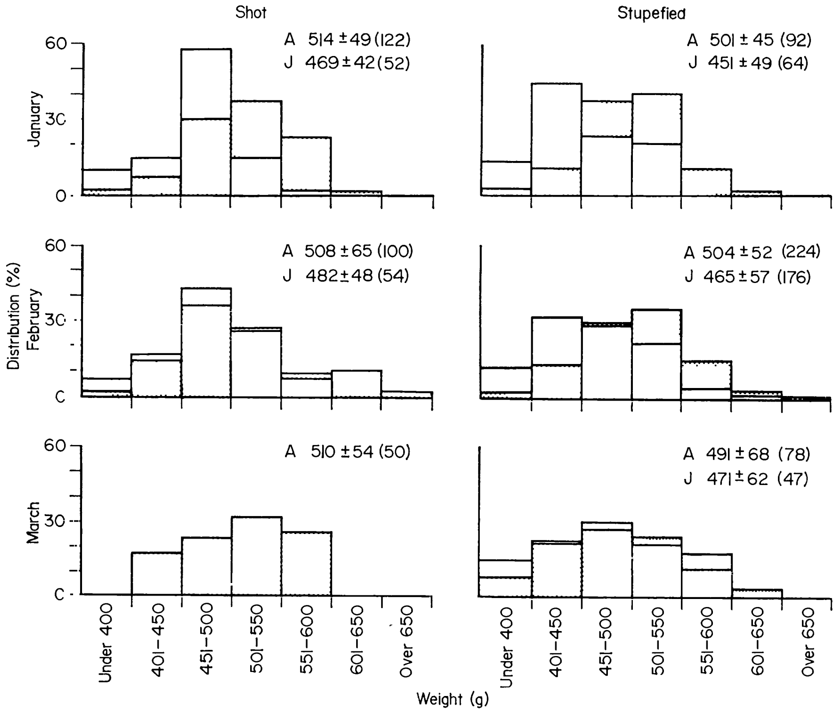

FIG. 12. Percentage weight distribution of wood-pigeons that were shot or captured with stupefying baits; 1964, 1969, 1970 records combined as comparable samples were obtained. stippled histograms, adults; open histograms, juveniles (<12 months old). Means ± S.D. (number in sample) are given. Significant differences between shot and stupefied juveniles were obtained in January (t_{114} = 2·107; $P<0·05$) and February (t_{228} = 2·251; $P<0·05$). There are differences in the frequency distribution of weights between shot and stupefied samples for adults in February (χ^2_4 = 13·747; $P<0·001$) but not in January (χ^2_3 = 6·051) and March (χ^2_3 = 2·998). Juvenile shot and stupefied samples differed in January (χ^2_3 = 16·466; $P<0·001$) but not in February (χ^2_3 = 7·045) or March (five juveniles only were shot, and are omitted from the histogram).

Both methods revealed an increase in the juvenile ratio in May when it is known from ringing recoveries that immigrants moved into the area. It is probable that immigrant juveniles favoured the pastures and leys where stupefying baits were localized. Those pigeons which fed in the woods and hedgerows which were less dependent on food supplies in the fields, were best sampled by shooting; the ratio of juveniles was much lower in shot samples from May until July. It is known from other studies (Murton 1965) that adults obtain territories in the woods in spring and that woodland rather than open arable farmland is the natural and favoured habitat of the species.

There was no difference in the mean weight of shot or stupefied adults in January but shot juveniles were, on average, 4% heavier than those caught with treated baits; the mean weight of shot juveniles was also higher in February (Fig. 12). In both months it is likely that the differences resulted from the fact that baits were mostly laid on fields of high clover density, where birds of low social status could establish themselves (cf. above and Murton *et al.* 1971). The mean weight of shot and stupefied adults did not differ in February but the variance of the former was significantly greater $F_{99}/_{223} = 1{\cdot}240$; $P < 0{\cdot}05$). Again it is likely that this was because the shot sample was drawn from a wider range of feeding habitats, for example, woodland, clover fields, fallows, old stubbles, than the baited birds. No differences in weight distribution were found in the case of pigeons examined in March (Fig. 12).

Although many trials with stupefied baits have been conducted records were not normally kept of the man-hour expenditure involved. But from January to March 1969, when Mr Edgar was shooting as many pigeons as he could in the study area (see Table 1) A.J.I. caught pigeons in the same area using baits treated with alpha-chloralose and recorded the costs involved. Excluding the time taken to walk from vehicle to field, also omitted from the shooting calculations, a total of 132 wood-pigeons was caught during 13·5 man-hours for which 80 kg of treated tic beans were used on two fields; pigeons were caught on only one of the sites. There is no reason why bait should not normally be distributed on many more fields, but in this case we did not want to interfere with the freedom of the shooter. This was, therefore, a conservative estimate of the efficiency of baiting procedures and the results compare the efficiency of two experts. The shooter required 0·23 man-hours to kill each pigeon but the baiting techniques needed only 0·1 man-hours. The tic beans plus alpha-chloralose used cost 8p/pigeon, giving a total cost of 13p/bird. This is nearly half of the cost to shoot a bird. The total cost of shooting or use of baits includes the time involved in reaching and leaving the site and carrying equipment and pigeons; the time of spreading bait is also included but the cost of erecting a shooting hide is not. Evidently baiting is a cheaper method of catching and killing pigeons than shooting. From a crop protection viewpoint, shooting has the additional advantage that vulnerable fields can be guarded by the scaring effect of the gunner.

NATIONAL EFFECTS OF CHANGES IN SHOOTING POLICY

Alterations in the seasonal pattern of mortality caused by changes in shooting policy can be judged at national level from the recoveries of birds ringed under the British Trust for Ornithology scheme (Fig. 13). Also, since the age at recovery was known the proportion of pigeons shot each month that were less than 12 months old can be delimited (Fig. 11). There was a consistent tendency for a higher proportion of juveniles to be killed nationally than at Carlton. This was probably because we were conscious of the need to avoid bias and relatively few shooters attempted to sample all habitats in the study area. But nationally many inexperienced guns are involved and these are not allowed to shoot in game preserves and probably concentrate too much on marginal habitats. Moreover, sites such as cabbage fields, where pigeons cause economic damage, are marginal habitats and they attract young birds displaced from more favoured areas. After March, juveniles which had completed the moult could not always be identified on plumage criteria and so some were probably incorrectly classified as adults when they were in fact less than 12 months old. Obviously if subjects were ringed as nestlings, their age on recovery was accurately known and the ringing recoveries are free from this bias.

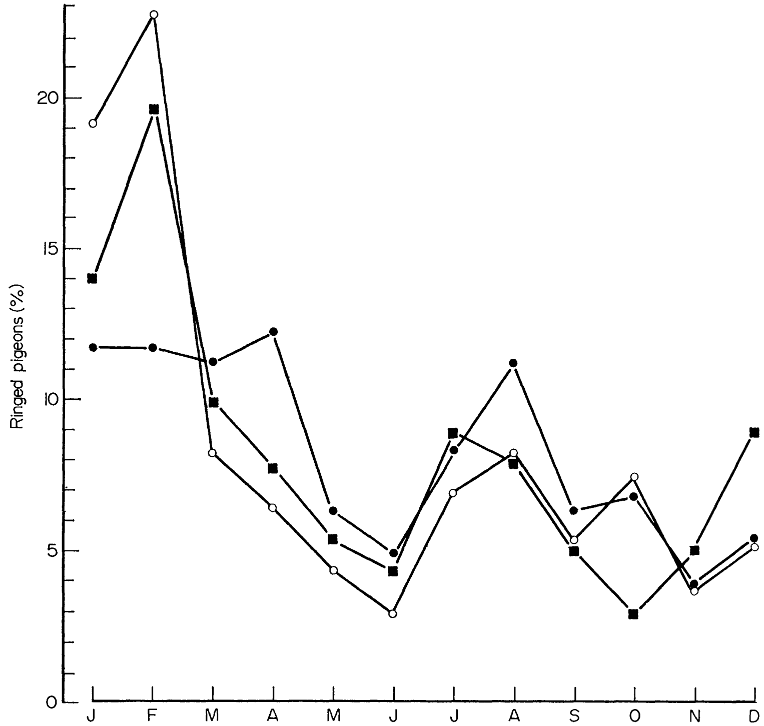

FIG. 13. Percentage distribution of ringed wood-pigeons which were shot; ●, shot between 1911 and 1952 (205 birds); ○, shot between 1953 and 1964, i.e., years of winter battue shoots (376 birds); ■, shot 1965–70 after support for winter battue shoots was withdrawn but subsidized cartridges remained available (413 birds).

Prior to 1953, there was a slight peak in shooting mortality in August, presumably because farmers, game-keepers and their associates shot birds at harvest and as they flighted to the stooked corn. The shooting pressure did not vary much between September and March, and employees on the estates were mostly involved. Thus pigeons will have been killed incidently during partridge shoots and pheasant drives over this period while gamekeepers probably contributed most of the remaining birds. The contribution from specialist decoy gunners was likely to have been small but consistent and such guns may have caused the peak in birds killed in April as wood-pigeons decoy well to the spring sowings.

Official support for the organized battue shooting of birds returning to roost was motivated by the belief that concerted efforts by many people would disturb the birds and keep them on the move causing more to be at risk of shooting. The subsidy scheme introduced in 1953 was administered through the County Pests Officers, who encouraged these evening shoots. But game interests did not allow strangers on the estates until after the pheasant shooting season and so battue shoots were concentrated into the period from mid-January until early March: thereafter, the light evenings brought counter attractions and also the onset of the pheasant breeding season. Fig. 13 shows that during the period 1953–64, 41% of all pigeons shot were killed in January and February, compared with only 23% before the introduction of the subsidy scheme. The subsidy was withdrawn from battue shooting in 1965 but half-price cartridges could still be obtained for other methods until 1969, through the Rabbit Clearance Societies. Although battue shoots were officially discouraged in favour of 'lone-wolf' decoy guns, to some extent, people have continued to follow the habits of the previous ten years as Fig. 13 shows. The current pattern of shooting mortality will doubtless be found to have changed again when sufficient records have accumulated for further analysis.

DISCUSSION

Although the studies described here had an economic purpose, one aspect of the research has theoretical implications in the context of the natural control of animal populations. It has been suggested that various behavioural conventions, including the flock habit and territorial activity serve to limit population size before resources become absolutely limiting (Koskimies 1955; Kalela 1957; Wynne-Edwards 1962). Thus the peck order or dominance hierarchy noted in feeding flocks has been viewed as mechanism for self-regulation of the population enabling resources to be distributed to best advantage and over-exploitation prevented. A contrary argument in the case of the wood-pigeon asserts that the flock habit maximizes population size for it improves the survival expectation of the individual (Murton, Isaacson & Westwood 1971). The amount of clover determined the number of pigeons which could live and survive at Carlton in winter. Shooting killed some birds which would otherwise have eaten food before dying and in this way resources were conserved to better advantage for the survivors. It follows that an efficient self-regulating mechanism should have achieved the same kind of result, but no such effect was seen. Winter mortality was the key-factor determining the way in which numbers fluctuated from year to year, while in turn the food supply determined the amount of winter mortality. Therefore, shooting at the level investigated must have reduced mortality rather than increased it. We suggest that natural selection has failed to produce a mechanism bringing the same benefits to the population as artificial culling because no means exist whereby the individual bird can be sacrificed for the benefit of the group.

Shooting for crop protection can only be justified in those circumstances where pigeons are prevented from attacking a vulnerable crop, and to a large extent the crop protection value of shooting depends on it acting as a scaring mechanism. It seems likely that more efficient and less costly scaring mechanisms are available. Paradoxically, because battue shooting reduced winter competition and allowed more birds to survive until spring it probably increased the risks of crop damage once the winter season of limiting resources was passed. In addition, winter battue shooting was more costly in man-hours and cartridge expenditure than decoy shooting (Table 2).

The scale of mortality due to shooting achieved to date, has been insufficient to hold population size below the level determined by food resources. If population control were made an objective more efficient ways of killing pigeons should be adopted. Alternatively, from a sporting viewpoint the wood-pigeon could be managed as a valuable resource, in which case the past level of shooting was below the optimum for maximum exploitation; perhaps an increase of one-half to three-quarters of the past annual shooting effort could have been tolerated without detriment to stocks. However, the decline in numbers of this species, first noted in 1968, has continued so that in 1973 the breeding population was about one-quarter of the level pertaining during the early years of the study. The decline has been the result of changes in arable farming methods which have led to a loss of leys and pastures and hence of clover stocks. The role of shooting in these changed circumstances has yet to be defined.

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The study would have been impossible without the splendid co-operation of Mr W. H. Edgar—we know he enjoyed his task even if at times we frustrated his prospects of achieving a good bag. We thank Dr J. P. Dempster for critically reading a draft of this manuscript, his suggestions for its improvement being gratefully accepted.

SUMMARY

(1) A wood-pigeon (*Columba palumbus*) population and its clover and grain food supply was censused from 1958 until 1970. During the first six years, winter battue shoots were held between late January until early March and large numbers of birds were killed as they returned to roost. No shooting occurred during the next three years and then an intensive experimental programme of decoy shooting by one man was monitored throughout the last three years.

(2) Shooting did not increase the total amount of winter mortality above the level experienced in the absence of shooting. The number of wood-pigeons in autumn and winter was determined by the amount of grain on cereal stubbles, or clover on leys and pastures, respectively, and immigrants moved in to take advantage of any unexploited food resource.

(3) There was no increase in pigeon numbers following abolition of battue shoots in 1965. Ringing records show that a higher proportion of recovered pigeons were found dead instead of being shot, suggesting that birds which previously were shot before dying of food shortage now succumbed for natural causes.

(4) In 1968–69 the average cost in terms of man-hours and cartridges for an expert decoy gunner to kill one pigeon was £0.24. It cost £0.13 to kill a pigeon with stupefying baits (0.10 man-hours/bird instead of 0.23 man-hours for shooting). For shooting to affect population size, a cost of about £0.50/bird would probably be realistic, assuming sufficient guns were available.

(5) For a given number of dead pigeon-decoys the percentage of passing pigeons at risk which responded, decreased as flock size increased as did the percentage shot. Ignoring any scaring benefit, decoy shooting is most effective as a means of killing pigeons when single birds or small flocks are at risk. An increase in the number of dead pigeon decoys with closed wings, to about eighty or, with open wings to about forty, led to an increase in the percentage response from live birds and hence numbers shot, but with more decoys pigeons were repelled. Within the ranges defined (0–80 and 0–40) there was no difference in the effectiveness of dead pigeons with closed or open wings. It is estimated that 7% of live pigeons at risk are killed with five closed-wing decoys, 14% with twenty such decoys and 23% (the maximum) with eighty decoys. Artificial decoys were 13–46% less useful than dead pigeons depending on the number used.

(6) A comparison is made of the age and weight distribution of shot wood-pigeons with those captured by the use of stupefying baits and differences are discussed. Variations in the seasonal pattern of shooting mortality consequent on changes in official policy and bounty incentives are examined by an analysis of those recoveries of ringed birds which had been shot.

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