

# THE RELATIONSHIPS BETWEEN WOOD-PIGEONS AND THEIR CLOVER FOOD SUPPLY AND THE MECHANISM OF POPULATION CONTROL

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## 1. INTRODUCTION

Other papers (Murton, Westwood & Isaacson 1964a; Murton 1965a) have discussed the factors regulating population size in the wood-pigeon (*Columba palumbus*) in a study area in Cambridgeshire. It was shown that, following a post-breeding season population peak, availability of grain on autumn stubbles determined the number of birds surviving in early December. On average most of the annual population reduction occurred over this period, juveniles being mainly lost from the area apparently as a result of direct starvation or emigration motivated by food shortage. A further variable decrease in numbers occurred in February or March apparently dependent on clover availability but thereafter food was not a limiting factor. Although other possible regulatory factors such as shooting and disease were examined they were not considered important and it was concluded that availability of food was the main factor limiting wood-pigeon numbers, at least in the study area. The reproductive rate seemed always the maximum that the birds could achieve and it did not limit winter population size (Murton & Isaacson 1964).

The purpose of the present paper is to examine more closely the relationships between wood-pigeons and their clover food supply. As before, the research was done in the study area of 2647 ac at Carlton near Newmarket, Suffolk, or in nearby areas where around 95% of the birds' diet in the period December (sometimes November) to March comprises clover leaves, the remainder being weed and grass leaves (Murton, Westwood

& Isaacson 1964b). Elsewhere (Murton, Isaacson & Westwood, 1963a) we have described some quantitative relationships between wood-pigeons and their grain and clover foods which are pertinent to the work described here.

## 2. METHODS

Three of the methods applicable to this study were described in detail and some results given in the above papers; these can be summarized as follows:

1. A regular census of the wood-pigeons in the study area based on direct field counts (Murton *et al.* 1964a).

2. Repeated measurements of clover leaf availability done by counting the number of leaves in random 1 ft square samples throughout the area (Murton *et al.* 1964a). Leaves partly eaten by pigeons could be distinguished by their characteristic torn appearance from occasional insect attack—e.g. from clover weevils (*Hypera nigrirostris*)—while leaves dying through frost damage or other causes could be distinguished by their brown withered appearance. A completely defoliated leaf-stalk was also recognizable for a variable period, but withering and new growth eventually made it impossible to identify such damage. The leaf count technique was suitable for examining the intensity of wood-pigeon attack under different conditions in comparable seasons but it did not provide an absolute measurement of feeding intensity except for limited periods or in special circumstances. The problem was made more difficult because a variable amount of clover growth occurs at all seasons so that leaves lost to pigeons were continuously replaced, this being particularly the case in mild winters.

Cattle and/or sheep were kept on some of the clover sites, and their grazing habits and the season when they were allowed access to the fields had variable effects on the clovers. On pastures, any lack of winter grazing enabled grasses to grow at the expense of clovers which became suffocated and lost; conversely, heavy grazing facilitated clover growth. Cattle graze an area more uniformly than sheep which are relatively selective (see, for example, Arnold 1964; Hughes, Milner & Dale 1964, and references quoted). Thus the species of farm stock also affected clover yield. Nevertheless, in mid-winter on pastures, when the clover leaves were lying prostrate on the soil, cattle did not feed closely enough to the ground to remove the leaves and even sheep were frequently unable to reach the clover. It was unusual for stock grazing to be allowed on leys in the winter as these were kept for summer hay and silage production, so stock grazing on these sites was usually of no importance. Rabbits (*Oryctolagus cuniculus*) have been virtually absent in the area since the advent of myxomatosis and hares (*Lepus europaeus*) have not been noticed to do much grazing on the sites. Furthermore, during the census counts of pigeons every hare seen has been recorded and the data show that this animal was more usually seen on waste land, rough grazing, arable or in growing root crops and not often on the pastures which were possibly not its main feeding grounds. While grazing by wild and domestic mammal species, including the small rodents, will have had some effect on clover availability this does not detract from the validity of the observations. Our concern was the amount of clover actually present and available for the pigeons to eat and this was measured by the sampling technique employed.

3. Numerous repeated watches were made of feeding birds and their behaviour recorded. Their feeding rates were calculated by counting the number of feeding pecks and paces (the best indication of the area searched for food) for known times (Murton *et al.* 1963a). Most work of this sort was done from a vehicle using a telescope or binoculars

as was the case for other watches of flock feeding and behaviour, and the birds soon behaved naturally even if there was some initial disturbance.

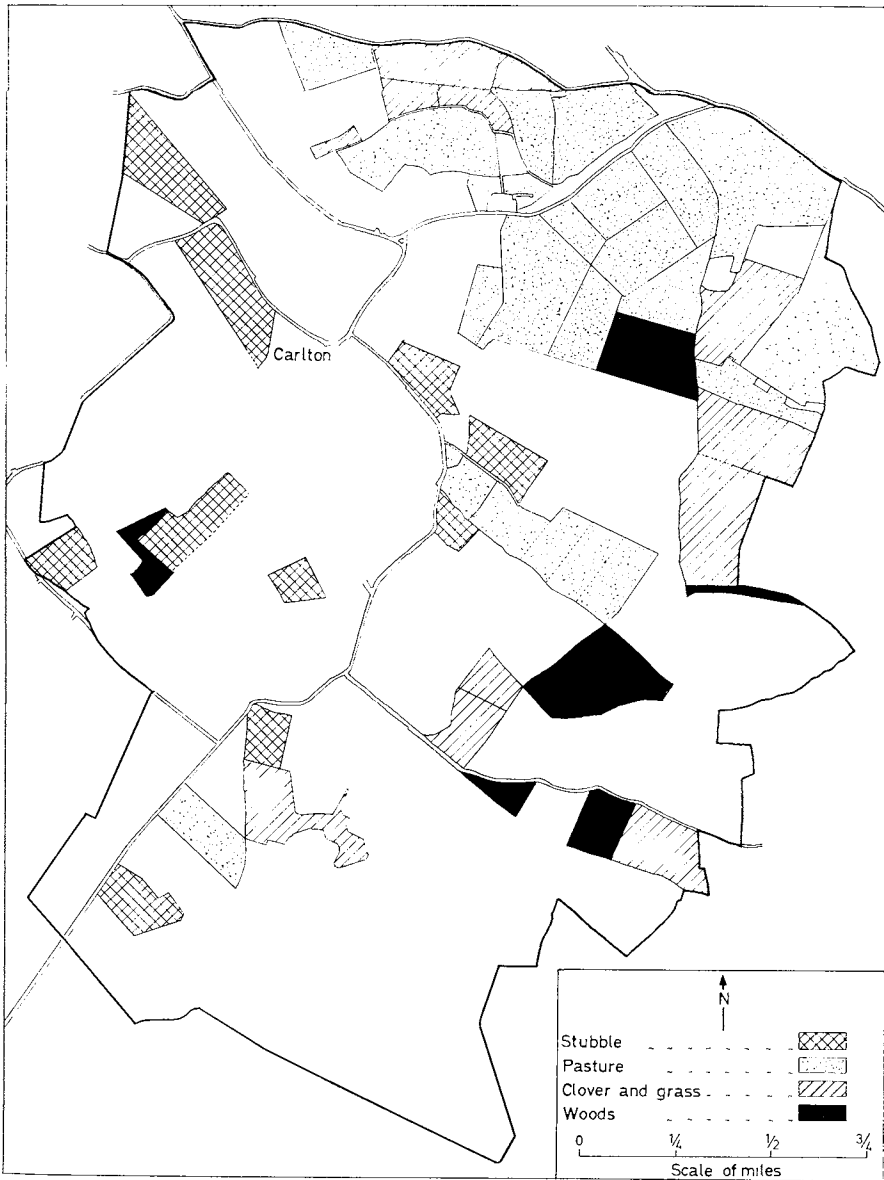


FIG. 1. The clover feeding grounds available for wood-pigeons in the Carlton study area in the winter 1961-62.

The following techniques were specifically adopted for this study:

4. For some accurate measurements of the impact of wood-pigeons on the clover stocks, enclosures were erected on certain fields to prevent access by the birds, and clover density was compared within the cages and on nearby unprotected but marked plots where the birds were able to feed normally. Care was taken not to create a favourable micro-climate because even the flimsiest cage can increase the water supply by dripping after

rain or by reducing air flow and frost entry. At first we used very light cages of black cotton supported on bamboo canes; these were usually sufficient to deter pigeons (occasionally, however, hungry birds were not frightened by these structures) but on fields where grazing sheep or cattle were kept the cages were soon knocked down by the animals. For later work such cages were surrounded by barbed wire or the cages were constructed of heavy corner posts surrounded by wire netting whilst tarred string was used as sparingly as possible on the tops.

5. Other methods were employed in the study depending on special needs: for example, birds were sometimes counted regularly on only a few fields; samples were shot, weighed and examined for body condition; numerous trials were done with stupefying baits, and birds captured were either marked and released or killed for detailed examinations.

Three main categories of clover site have been defined. The first being 'clover-leys', which were cereal undersowings of red clover (*Trifolium pratense*) in their first winter season and cereal stubble was present. The second being these same leys in their second season, the stubble having rotted away, grass species having become established and displaced some of the red clover which in turn was partly replaced by white clover (*T. repens*). Such sites were now termed 'clover and grass sites'. In this category could be included sites initially planted as clover and grass mixtures. In the third category were the 'pastures' represented by semi-permanent grassland characterized by the small-leaved white clover and some wild species and various weeds. Ecologically the pastures were reasonably stable climax plant communities. Differences in clover leaf size or in nutritive value were not allowed for in this study, although seasonal or local variations could possibly be important. Specific differences were certainly important and red clover samples weighed 3.78 times as much as white clover samples, so for comparative work the sampling results for the former were reduced by this factor when appropriate (see text). Clover samples collected from four different leys and from one pasture in February 1961 were kindly analysed by Dr C. J. L. Baker, nutrition chemist of the National Agricultural Advisory Service, and the results are given in Appendix 1. There were some fairly large differences between fields, but unfortunately it was not possible to study more sites.

An indication of the distribution of the clover feeding grounds in the study area is shown in Fig. 1 for the winter of 1961–62. The pattern was similar in the other years, most pastures being located in the same sites, although undersown clovers were found in different sites each year following the rotation of cereal crops. The proportionate acreage supporting clover crops remained reasonable constant over the years of study and ranged from 29% to 36% of the whole area.

### 3. THE EFFECT OF WOOD-PIGEONS ON CLOVER AVAILABILITY

#### (a) *Seasonal changes in clover density*

The amount of clover available at the beginning of winter depends upon the amount sown, which is decided by animal stock requirements and partly by weather conditions. For example, a wet autumn means that less winter wheat is planted and more spring barley, and it is usually only spring-planted cereals that are undersown with clover. But treatment of the field and the amount of stock grazing or silage cutting can have considerable effects on the clover stocks which are always directly influenced by soil fertility and condition and by weather factors. Fig. 2 depicts the various changes taking place on three fields over 2½ years, by detailing clover leaf density both inside one control cage of 12 × 3 yd on each field, and on nearby unprotected plots. The results reflect the changes

that occurred throughout the whole study area. In general, clover stocks were highest in early summer from May to July, when the highest level of clover density achieved and the duration for which high densities persisted was to a large extent determined by animal

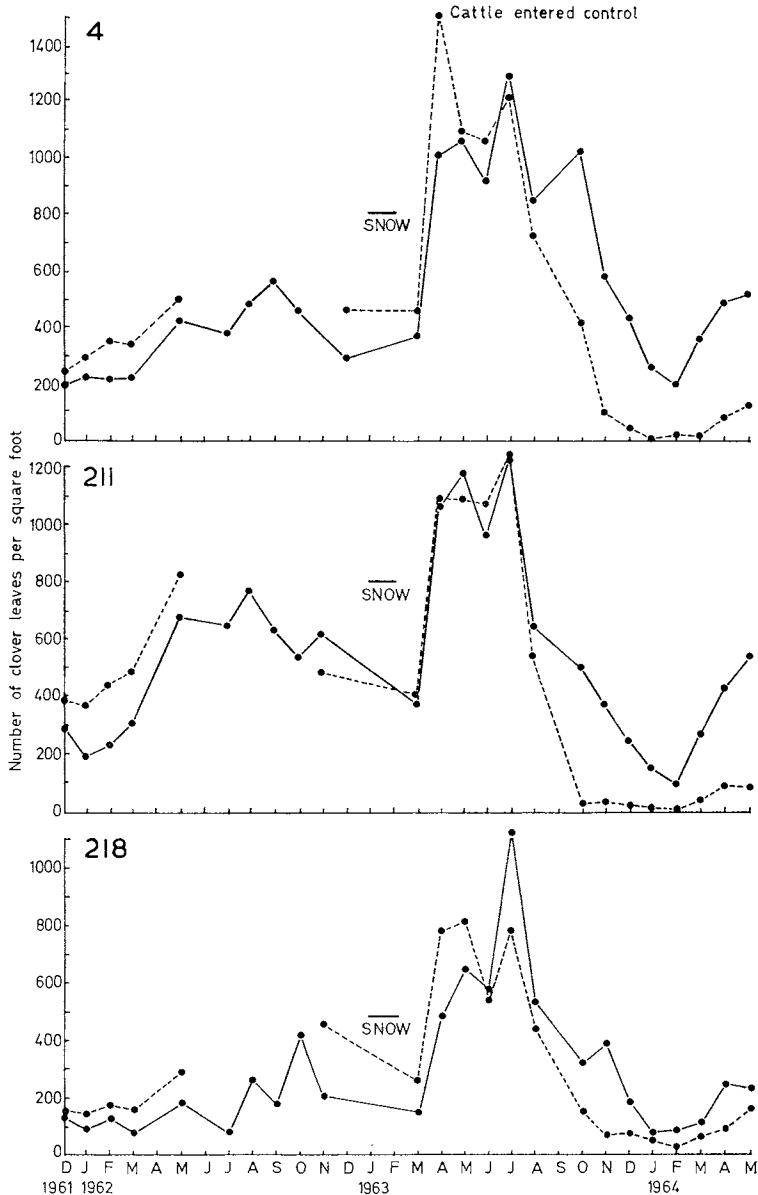


FIG. 2. Variations in clover density inside (---) and outside (—) protective control cages on three pastures from December 1961 to May 1964. On field 4 cattle gained temporary access to the control plot during the March to May 1963 period.

grazing and by cutting for hay or silage. The number of clover leaves then decreased in mid-summer when the plants had flowered and formed seed and when new growth was hindered by lack of rain. A resurgence of fresh growth took place from July to September

with an increase in rainfall, after which the top-growth partly died in the cooler days of autumn, this process being accelerated if there was much frost. Minimum clover stocks were found in February and March but with milder weather in spring there was a rapid flush of top-growth from a healthy root system. The amount of clover in winter was not greatly affected by stock grazing but in spring when the plants reached 6 in. in height domestic animals did remove large quantities as can be seen in the graph for field 4 in March–May period 1963 when cattle gained temporary access to the control plot.

Wood-pigeons begin feeding almost exclusively on the clovers when stubble grain vanishes, sometime in November or December (Murton *et al.* 1964b). Their depredations are most intense at the time when stocks are lowest, and they may regularly cause reductions of over 50% of what would normally be present. Pigeons desert the clover in

Table 1. *Changes in clover density on two fields in 1961 caused by weathering and wood-pigeon feeding*

¼ month of observation	Field 45			Field FL		
	No. of leaves per square foot in Cage	No. of leaves per square foot in Field	% difference between cage and field	No. of leaves per square foot in Cage	No. of leaves per square foot in Field	% difference between cage and field
January 1	157	166 (4)	+6	213	222 (8)	+4
February 1	106	43 (55)	-60	168	48 (66)	-71
March 3	191	174 (28)	-9	464	328 (20)	-29
% difference between January 1 and February 1	-32	-74		-21	-78	
% difference between February 1 and March 3	+80	+305		+176	+583	

Figures in parentheses refer to the percentage of clover that could be seen to have been taken by pigeons judged by the evidence of defoliated leaf stems.

See text for discussion.

spring when cereals and other foods become available and throughout the summer take only a small proportion of what is present (Murton *et al.* 1964a).

During 1963 and subsequently the grass inside the cages was ungrazed by cattle and it grew to such an extent that the slower growing clover gradually disappeared. The situation is comparable with the loss of certain grassland plant species following myxomatosis and the consequent inability of the rabbit population to graze down the high vegetation (Thomas 1960). Thus cage work over a protracted period on pastures is of limited value because not only is pigeon grazing prevented but also that by sheep and cattle. Ideally cage experiments to isolate and measure only wood-pigeon damage are best confined to one season of winter damage, after which new cages should be erected on fresh areas.

#### (b) *Estimation of damage*

To measure the impact of pigeons on a clover crop more effectively three cages of 12 × 3 yd were erected on each of two fields on 21 December 1960. Both fields were clover leys and no livestock grazing took place although many pigeons fed. During the first weeks of January and February and in the third week of March the number of clover leaves present and the number attacked were then counted in four samples each 1 yd square (total of twelve samples for each field) inside the cages, and on four samples in nearby unprotected plots (again twelve samples for each field). Completely eaten leaves were distinguished from those partly eaten but both categories have been lumped in Table 1

where the results have been converted to the number of leaves present or attacked per square foot.

Reference to the table shows that the unprotected plots on field 45 originally contained 6% more clover than the controls in early January. After 1 month the number of clover leaves in the controls decreased by 32% and in the experimental plots by 74%. The decrease in the controls was caused by weathering and frost damage: thus if the same frost damage occurred over the rest of the field the real loss caused by wood-pigeons was  $74 - 32 = 42\%$ . Direct inspection of the plots suggested that 55% of the leaves had been attacked by pigeons to some degree, but as in January 4% had already gone, a better estimate would perhaps be 51%. The differences probably arise because there may have been a little clover growth over the period, and whereas an undamaged leaf could be lost through frost attack and not be recorded, an eaten or partly eaten leaf so affected would be recorded as attacked. The marking of individual leaves might have overcome this problem.

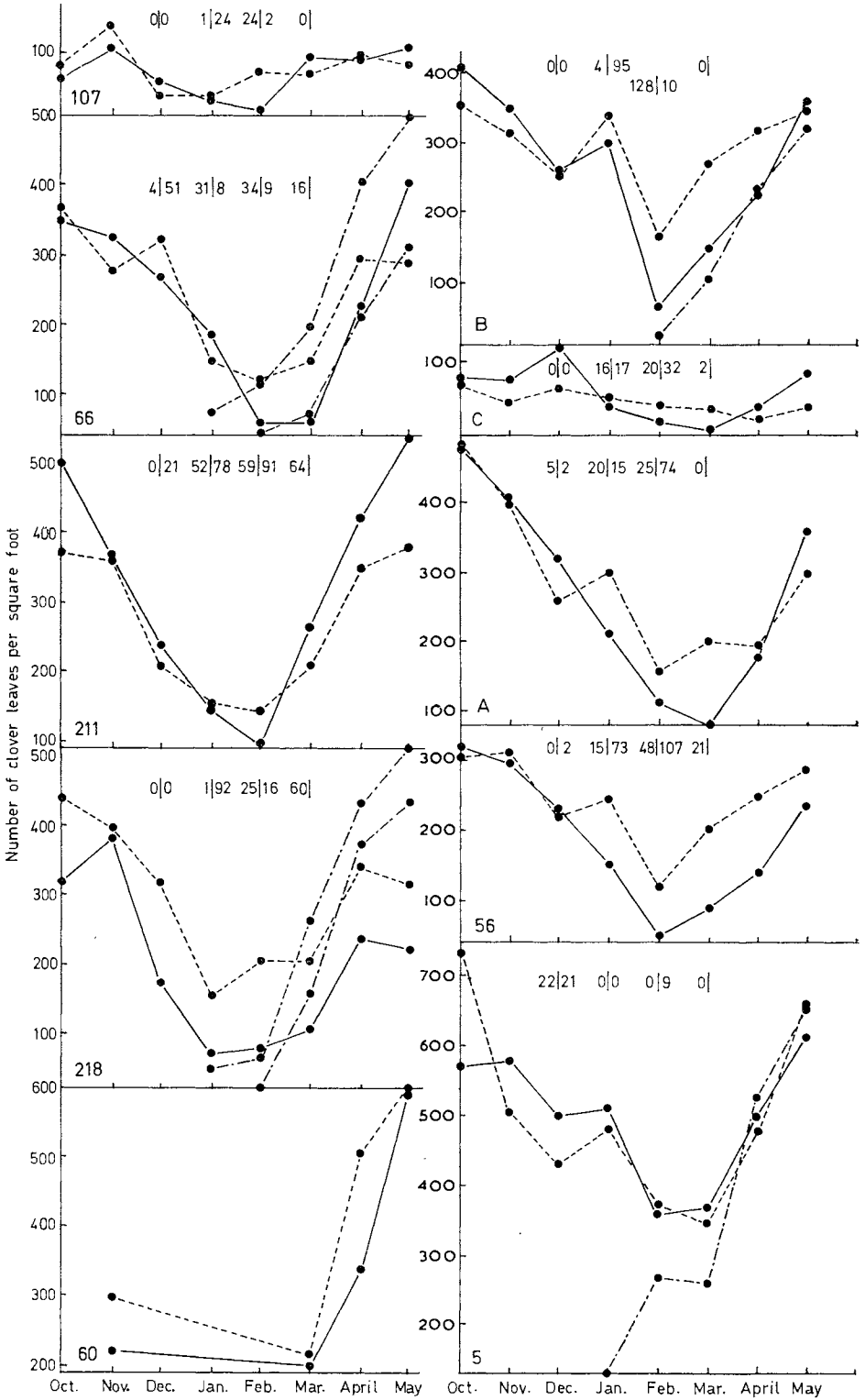
The proportionate difference in leaf number between the experimental and control plots on the same day was 60% but this datum is misleading because the proportionate change in leaf density in the control and experimental plots makes it unrepresentative of actual damage. The difference in the number of leaves actually present was  $106$  (experimental)  $- 43$  (control)  $= 63$ . This compares with a loss of  $123$  leaves/ft<sup>2</sup> in the control sites from January to February minus a loss of  $51$  in the experimental plots over the same period, to give an estimated loss through pigeons of  $72$  ( $123 - 51$ ). The same considerations could not be applied if appreciable clover growth had been occurring. However, it is likely that the plants were fairly dormant over the period reviewed, as the mean weekly temperature at the National Institute of Agricultural Botany, Cambridge (13 miles away) throughout the period 1 January to 4 February was  $3.6^{\circ}$  C. On field FL it seems that  $78 - 21 = 57\%$  of the leaves had been taken (21% lost through frost) while  $66 - 8 = 58\%$  could be recognized as eaten.

The number of birds on these fields was noted at approximately the same time each day and within 5 min for each of the two fields between 3 January and 10 February. There were twenty-five counts for field 45 and the mean number of pigeons seen per acre was 0.9 with a maximum of 6.8/ac on one day. On field FL the mean density was 2.0 pigeons per acre (twenty-two counts) with a maximum of 10.2/ac. There appeared to be a higher pigeon density where initial clover stocks were highest (see also below) and as proportionately more was lost, both fields were reduced to about the same density by early February.

Table 1 shows that by the third quarter of March there was virtually no difference between the control and experimental plots in field 45. Whereas clover yield in the protected plots had increased by 80%, the experimental plots showed a 305% increase. In other words, spring growth was proportionately greater on the extensively pruned plants and this compensated for heavy damage. Field FL had not recovered at this stage but was doing so when the experiment was finished.

Although wood-pigeons may take over 50% of the available clover crop in one month in winter this is a loss to the farmer only if the plants are required for winter feed. Summer feed and silage production seem to be uninfluenced by heavy winter pigeon grazing and this was also shown in another series of experiments done in 1963-64 and illustrated in Fig. 3, and for one trial undertaken in 1962-63. Details of grazing by farm stock are given in the caption to the figure. Only one cage of  $12 \times 3$  yd was erected on each field, and the herbage in part of the caged plots (about a quarter of each plot) was

Wood-pigeons and clover





cut with garden shears on three fields in January so that 49, 67 and 73% of the clover was removed together with the grass. Complete removal of the clover would have been too tedious, because even with garden shears it was not always possible to get beneath the clover. The amount of clover removed was determined from sample leaf counts made before and after cutting. The clover was also artificially reduced in the same way for the first time in February inside three cages (two cages were the same as those treated in January, although different areas were cut), by 65, 89 and 86%. The recovery rate of clover uninfluenced by pigeons could thus be examined. Again in spite of winter damage, although not such severe damage as that recorded in 1961, the average reductions on the fields from January to February being 33%, the crops recovered after the spring flush of vegetation and pigeons could not be held responsible for causing any permanent reductions in crop yield. Furthermore, the recovery rate of the artificially cut areas simulating extremely heavy damage was also so great that those areas cut in January had

Table 2. *Relationship between the index of clover availability in different years in the Carlton study area, the proportion eaten by wood-pigeons and their population size*

		Index of clover density	Index of no. leaves eaten	% leaves eaten	Maximum no. birds per 100 ac	Minimum no. birds per 100 ac
1961	February	1887	2855	60	125	117
	March	7504	1987	21	83	83†
1962	February	1676	826	33	70	50
	March	1779	1172	40	72	64
1963	February	0	0	0	1	1†
	March	1860	47	2	61	61†
1964	February	1132	—	33*	62	49

\* This figure was obtained by comparing the number of leaves outside and inside cages protecting the clover from pigeon attack (see text).

† In these months only one count was made compared with two in the others.

recovered by March and those cut in February by late April. In four out of six cases the cut areas eventually supported more clover than the uncut controls, but this may have been partly the result of cutting the grass at the same time. As before, the number of pigeons present in the various fields was counted at approximately the same time each day (between 13.00 and 15.00 hours). The results were averaged for each half month and the following numbers of days were available for each period: December, 5 (first half), 6 (second half); January, 9, 11; February, 8, 10; March, 10 (first half). The results are given in Fig. 3 and show the relationship between the period of pigeon feeding and the onset of obvious crop reductions.

Since 1961 every site in the study area supporting clover has been sampled and some details have already been published (Murton *et al.* 1964a). From the average clover density per square foot for the three different categories of clover site a quantity index was calculated by multiplying the average leaf density per square foot by the percentage

FIG. 3. Variations in clover density on nine clover sites in 1963–64 and on one field (No. 60) in 1962–63. —, Leaf density outside cage where wood-pigeons grazed (experimentals); ---, leaf density inside cages protecting crop from pigeon attack (controls); - - - -, leaf density in areas inside cages that were artificially cut in January or February. Fields 107, 66, 211 and 218 were pastures, the rest were clover leys. The average number of wood-pigeons recorded on each field is given for half-month periods. On fields A, B, C, 56, 5 and 60 no grazing by farm stock took place. Sheep grazing took place on the other fields as follows: 211, 4–27 February; 218, 4 to 28 February; 107, 9 December to 9 February; 66, 9 December to 4 February.

acreage supporting the particular clover category. In addition, but so far not described, an index of the clover attacked by the birds was obtained by multiplying the average number of attacked leaves per square foot with the percentage acreage as above. The data are given in Table 2 and from them it is possible to estimate the proportion of clover attacked, as was done for the experiments already described, but in this case the results are applicable on average to the whole study area and not single fields. The density of

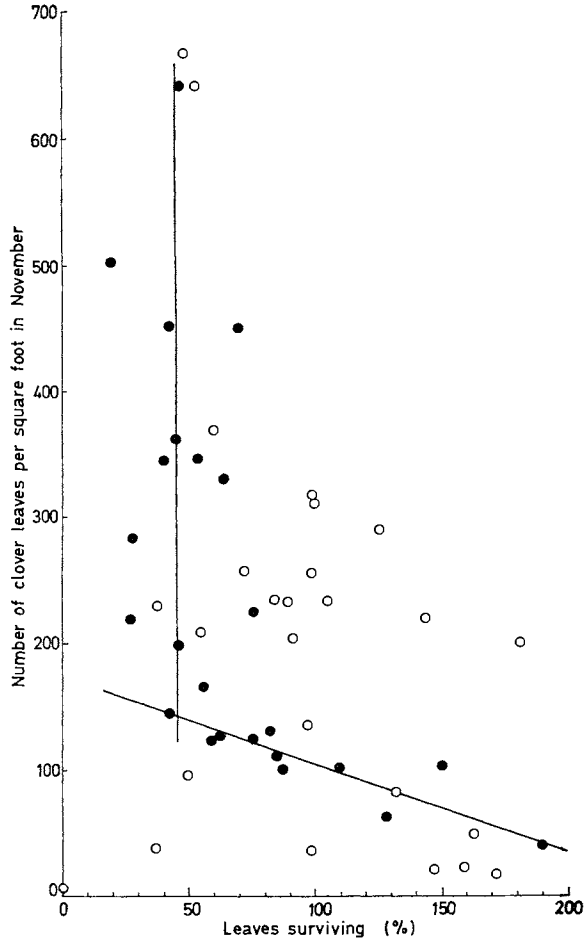


FIG. 4. The average number of clover leaves per square foot on different fields in November compared with the percentage surviving in the following late January to early February period 1962 (●) or early March period 1963 (○). The correlation coefficient  $r = -0.5309$ ,  $n = 23$  is significant in 1962 but not in 1963 ( $r = -0.3457$ ,  $n = 25$ ). One point for 1962 was omitted from the graph for space-saving reasons (leaves = 17, % = 394) and one in 1963 (leaves = 6, % = 533).

pigeons per 100 ac was also known from the census counts and the monthly maxima and minima are given in the table. In 1964 the clover eaten was not measured by direct inspection and so the estimate of damage for February has been calculated from Fig. 3 by comparing the difference between the January and February readings inside and outside the protected cages, as was done in Table 1. Both wood-pigeon numbers and the amount of clover were continuously changing and it should be remembered that the clover index in Table 2 indicates the situation at one instant of sampling only, while the number of

leaves eaten refers to the cumulative situation over one or two months. Even so, the data are informative in indicating that the heaviest apparent wood-pigeon damage is recorded with high pigeon populations and low clover indices. The table also shows that in most years there are insufficient birds available in March to take advantage of the improvement in clover supplies although some immigration may occur. 1963 will be considered in detail below.

(c) *The effect of clover density on wood-pigeon feeding*

The density of clover expressed as the number of leaves per square foot varied considerably between fields in the same or different years. In the winter of 1961–62 we compared the average number of leaves per square foot in November on pastures and clover and grass sites with the number on the same field in late January and early February, where data were available, and expressed this as the percentage leaves surviving of those originally present (Fig. 4). This was a season when on average the pigeons had eaten about one-third of the leaves available by about mid-February (Table 2). Fig. 4 indicates that in this season there was a relationship between initial leaf density and percentage leaf survival ( $r_{23} = -0.531$ ). But inspection of the figure strongly suggests that the points fall on two curves and the apparent best lines have been drawn by visual inspection. With the information available it seems that a change occurred with November leaf densities around 150 per square foot. Separate correlation coefficients were calculated for all values above or below this arbitrary figure. There was no correlation in leaf survival for points over 150 ( $r_{11} = -0.142$ ) but a highly significant one for values below ( $r_{10} = -0.870$ ). The difference in leaf number between November and January/February will have depended on a small amount of clover growth (mean temperature from December to February inclusive was  $5.7^{\circ}\text{C}$ ) less any leaf loss caused by pigeon feeding, weathering or natural decay. It would be expected that frost damage would be density-independent but that it might be related to the field location, for example, whether the field was on high ground or in a frost drainage basin. Moreover, if frost damage was related to leaf density it would tend to be less severe in areas of lush vegetation because the denser growth might afford more protection. Certainly a threshold above which density effects would cease to have significance would not be expected. Clover growth might be greater at low leaf densities owing to a lack of competition between leaves for light. But again a marked threshold effect would not be expected, while data obtained in 1962–63 (see below) militate against this suggestion. The distribution of grazing farm animals could not account for the above result and it is concluded that the pigeons removed more clover from the areas of higher density. The same relationships were found when leaf survival between November and December was compared, but of course fewer leaves had disappeared at this stage.

Support for the above view comes from the data in Table 3. The fields selected for the sample were not quite the same as for Fig. 4 because for five pastures and four clover and grass sites no readings were available for late December and hence these fields were omitted from the table. Conversely those fields included in Table 3 which also contribute to Fig. 4 are starred (as mentioned above stubble sites were omitted from Fig. 4 as were fields 217, 11c and 37 because no readings for the January/February period were available). These adjustments were made to ensure comparable samples and do not introduce any bias. Table 3 shows that the amount of clover in each field in November was correlated with the amount present in December, January and May, as might have been expected, although the correlation was less strong by May than in December. More

important there was a correlation between the number of leaves eaten by pigeons in December and the number available in November, and similarly between the number eaten in January and the number available in December. Because leaves were recorded as completely or half eaten, to determine the total eaten for each sample in Table 3 the number of half leaves was divided by 2 and this figure added to the number completely removed; a greater degree of accuracy was not feasible under field conditions. Although more leaves were eaten where more were available this was not apparently a density-dependent process. Hence when the figures in columns 5 and 6 of Table 3 were converted

Table 3. *Variations in clover density on different fields during the 1961-62 winter*

		Average number of leaves present per square foot				Average no. of leaves recorded eaten per square foot	
		Late November	Late December	Late January	Early May	Late December	Late January
		(1)	(2)	(3)	(4)	(5)	(6)
66	P*	504	192	-	283	213	-
209	P*	452	355	315	468	31	41
234	BS	449	274	-	313	21	-
227	BS	424	341	-	411	13	-
211	P*	348	291	189	673	20	78
4	P*	331	192	212	413	13	32
52	BS	286	189	-	137	8	-
6	P*	283	112	80	176	11	23
4B	P*	225	179	172	191	12	35
45A	BS	221	73	-	177	36	-
10	P*	219	102	-	104	47	-
218	P*	197	126	91	179	6	15
11A	CG*	165	153	92	116	18	51
11D	CG*	132	84	108	111	13	12
6A	P*	127	118	96	105	20	23
11B	CG*	126	101	80	121	13	55
5A	BS	119	66	-	63	12	-
6B	P*	112	116	169	423	5	8
9A	P*	101	91	-	86	36	-
216	CG*	101	62	111	139	5	19
217	P	100	64	-	43	3	-
215	P*	61	78	78	130	5	22
11C	P	48	42	-	295	1	-
37	P	48	36	-	-	1	-

\* Data for these fields are included in Fig. 4.

P, Pasture; BS, barley stubbles; CG, clover and grass.

The correlation coefficients between columns were: 1 and 2  $r = 0.863$   $n = 22$   
 1 and 3  $r = 0.784$   $n = 11$   
 1 and 4  $r = 0.592$   $n = 21$   
 1 and 5  $r = 0.518$   $n = 22$   
 2 and 6  $r = 0.598$   $n = 11$

to percentages of those in columns 1 and 2 respectively and tested for correlation with columns 1 and 2, none was found ( $r_{22} = 0.198$  and  $r_{11} = 0.239$ ). The fact that Fig. 4 suggests that proportionately less clover was removed at low clover densities while Table 3 indicates a straight and not density-dependent relationship could result from the inadequacy of our techniques. Thus relative leaf survival depends on the cumulative effect of all variables over a long period, whereas the number of leaves taken is a measure which becomes less valid with increase in interval between observations, especially if much new growth occurs.

The above results could be explained if at the higher clover densities either more pigeons

fed where clover stocks were highest—but not proportionately more pigeons—or alternatively that the birds fed for longer, but not proportionately longer, periods. Similarly with low clover densities either fewer pigeons must have fed or less time was spent in feeding, while Fig. 4 suggests that the feeding must have been proportionately less intense.

Similar observations on leaf survival were made in the 1962–63 winter (Fig. 4). In that year snow covered the clover fields from late December until early March and there was virtually no pigeon feeding (a little clover was taken by the birds in early December) over the period (Table 2). In this winter, leaf survival depended on growth and weather loss only, and with temperatures averaging under 1° C throughout December to February probably little growth occurred. Clearly percentage leaf survival was unrelated to density and it seems likely that this followed the absence of pigeon grazing. As in 1961–62 the actual number of leaves in the spring of 1963 (in March) was positively correlated with the number in the previous November ( $r_{26} = 0.807$ ).

(d) *The effect of clover density on wood-pigeon distribution*

In 1962 the distribution of feeding wood-pigeons in the study area was noted during three census counts made on 31 January and 1 and 2 February. Each field was considered a separate unit and the maximum number of pigeons seen feeding converted to the number per acre (Fig. 5). More pigeons were feeding where clover stocks were higher ( $r_{20} = 0.619$ ,  $P = 0.01$ – $0.001$ ). The same exercise was repeated in 1963 on 13 and 14 March when the snow had disappeared and pigeon numbers seemed to be low relative to clover stocks, and no such relationship was found ( $r_{16} = 0.083$ ). Similarly no significant correlation was found between clover and pigeon density on 25, 26 and 27 March (but see below).

The wood-pigeons were distributed in flocks and as these occupied only part of a field it seemed unlikely that the size of field limited the size of flock. It seems, therefore, justifiable also to compare total flock size (without converting the data to the number of birds per acre) with clover density. In 1962 the biggest flocks were located in areas with the highest clover density ( $r_{20} = 0.585$ ) but not on 13 and 14 March 1963 ( $r_{16} = 0.298$ ). However, the distribution of flock size on 25, 26 and 27 March was again related to clover density ( $r_{15} = 0.519$ ) by which time there had been an influx of pigeons into the area and numbers rose from a maximum of 1 per 100 ac in February to 61 per 100 ac in late March.

So far no account has been taken of those fields where clover was available but no pigeons were seen feeding. There could have existed an unexploited food source, although general observations and the disappearance of clover leaves suggested that birds were not avoiding suitable feeding grounds for very long. There are many difficulties attached to the evaluation of work of this sort; for instance, it can happen that fields of high food density are unexploited because pigeons are disturbed by farm workers or are too near houses. However, in January and February 1964 six independent census counts of pigeons were made in the study area and six between January and early March 1965, at times when few spring sowings had been planted and when stubble grain had vanished (Table 4). Only those birds seen actually feeding on clover sites were used in compiling the table, birds recorded resting, flying or in hedgerows being omitted. The clover density on all fields was known from the monthly clover counts and it was thus possible to compare pigeon and food distribution using the fields as individual units. Table 4 is a summary of the results in that the average bird density is given for all fields combined which

had clover densities either above or below an arbitrarily defined value of 100 leaves/ft<sup>2</sup>, during the months when the bird counts were made. (The original unsummarized data are given in Appendices 2 and 3.) In both years in January most of the flocks seemed to be associated with fields of high clover density and this was noticeably so in 1965. Clover densities had declined by February, whereas the total pigeon population stayed roughly constant. To compensate, more pigeons had to feed at the lower clover densities and

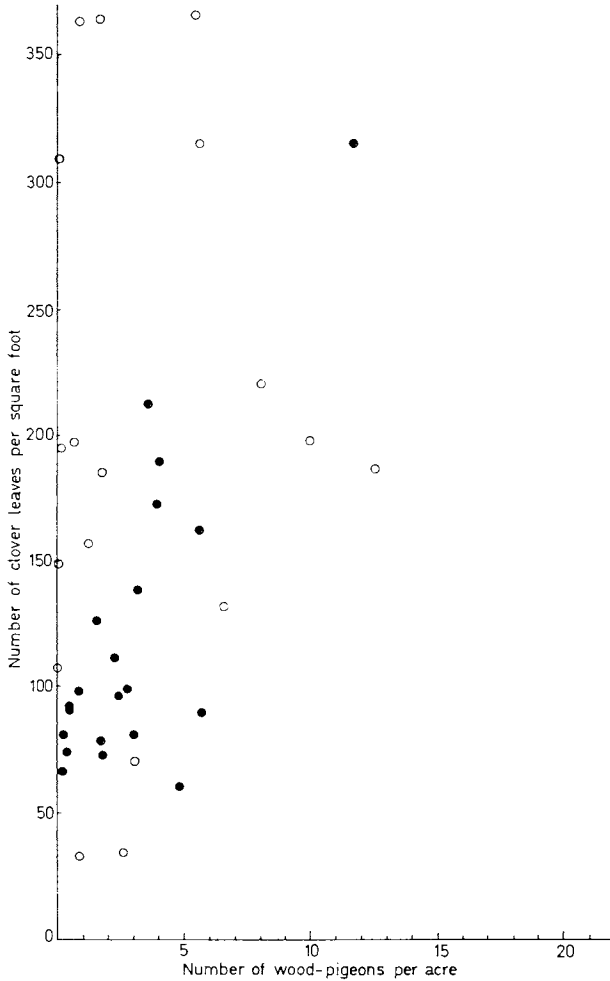


FIG. 5. The number of wood-pigeons per acre on different fields in relation to clover density in January to February 1962 (●) ( $r = 0.6186$ ,  $n = 20$ ); early March 1963 (○) ( $r = 0.0825$ ,  $n = 16$ ).

pigeon density increased on these sites. There was an overall loss of birds in late February 1964 but whereas pigeon density remained constant at clover densities above 100 it fell sharply on the poorer fields. In 1964 it seemed that pigeon mortality (or enforced emigration) occurred only in those flocks feeding on the poorer sites. This pattern was not clearly shown in 1965 and apart from an increase in bird density at low clover values in February the general picture was of pigeon loss at all clover densities by early March. The field observations for 11 March 1965 were not entirely satisfactory because many pigeons were still in the woods when the count was made and for this reason details for the count done

on the 10 March alone are separated in parentheses in Table 4. There is some suggestion that bird density at high clover values fell to a level comparable with that recorded in 1964 (around 1.4/ac) and there was approximately the same amount and distribution of clover in the two years. Better agreement between bird counts and clover readings might have been forthcoming had intermediate observations been possible and if the clover counts could have been done at exactly the same time as the bird counts, but the labour involved prevented this.

Table 4. *Distribution of feeding wood-pigeons at Carlton in the winters 1964 and 1965*

Date census counts made*	Average number clover leaves per square foot	No. clover fields available	Acreage of clover fields	No. separate pigeon flocks†		Average no. birds per acre‡
1964						
7 and 9 January	Over 100	17	383	7	6	1.4
	Under 100	26	362	5	5	1.2
5 and 6 February	Over 100	12	277	8	6	1.4
	Under 100	31	468	10	9	1.5
19 and 20 February	Over 100	12	277	7	6	1.5
	Under 100	31	468	10	9	0.8
1965						
13 and 14 January	Over 100	21	448	7	9	3.2
	Under 100	26	355	1	4	0.6
10 and 11 February	Over 100	11	240	7	4	2.4
	Under 100	36	563	12	11	2.0
10 and 11 March	Over 100	16	382	8	6	0.9 (1.4)§
	Under 100	30	414	8	8	1.2 (1.0)

\* Two census counts were made on consecutive days. Only birds seen feeding on clover sites are included.

† The left-hand figures are the number of flocks seen on the first day count, the right-hand column those on the second. Thus on 7 January there were seven flocks on fields with clover density above 100 leaves/ft<sup>2</sup> and five flocks on fields with a clover density below this value, i.e. a total of twelve flocks in the study area.

‡ Average density for the two separate counts combined.

§ Figures in parentheses refer to count done on 10 March only.

Some of the seemingly anomalous results in the table might partly be accounted for by the distribution of the fields. For example, in 1965 field 244 was the only clover feeding ground available for those birds feeding in the south-west corner of the study area, which would normally have roosted in North wood (a wood lying roughly in the position of the words 'stubble' and 'pasture' in the key of Fig. 1). The flock feeding on this field markedly depressed clover density over the winter and the fact that the birds did not leave the field could be attributed to the absence of any other reasonably accessible source of food. Effects of this sort may well have operated but the fact that pigeons were sometimes distributed according to their food supplies but at other times were not, can be explained more satisfactorily, and this will be done in Section 6 after some other observations have been described.

#### 4. THE BEHAVIOUR OF WOOD-PIGEONS WHEN FEEDING ON CLOVER

Wood-pigeons are markedly gregarious when feeding, and even their other activities are usually performed in groups, outside the breeding season. In January and February 1961 when six census counts were made in the study area and a grand total of 14 474 pigeons was recorded feeding, flying or doing other things only 0.2% were noted as single birds

and only 0.6% in flocks of less than five. Similarly, in 1962 seven census counts produced 8395 pigeons and only 0.3% of the birds were seen singly and 0.7% in flocks of under five individuals. Throughout the two January/February periods mean flock size ranged between twenty-five and 115 and the average number of flocks in the study area was forty-two (including single birds as flocks) in 1961 and twenty-five in 1962. Further information for feeding birds can be deduced from Table 4.

The following observations were made to help understand the significance of the flocking habit bearing in mind that any relationships between the birds and their clover food supply had apparently to operate via their social habit. Thus the birds' distribution which sometimes was and sometimes was not related to clover density had to be explained on the basis of gregarious behaviour, as did also mortality which will be discussed in Section 5.

#### (a) *Flight behaviour*

In order to discover the degree of flock integration we watched flocks of feeding wood-pigeons and recorded the behaviour of birds flying overhead (Table 5). Thus, when watching flocks ranging from one to twenty individuals (on four separate occasions), a

Table 5. *The behaviour of flying wood-pigeons on sighting a feeding flock*

Size of feeding flock	No. of flocks observed	No. of birds arriving in the vicinity of a feeding flock	Percentage of those birds arriving which:					
			Showed no reaction	Dipped or circled only	Alighted at the flock in the:			
					Rear	Middle	Front	
1-20	4	382	35	19	22	3	21	
21-100	7	282	10	2	35	4	49	
101-150	3	263	0	0	29	25	46	
Total and mean	14	927	18	8	28	10	36	

total of 382 pigeons arrived (often as single individuals) in the air within sighting range. Thirty-five per cent of these birds gave no reaction, the rest either circled or dipped over the feeding birds and then continued their flight (19%) or they settled in the flock. The larger the feeding flock the fewer the number of pigeons that showed no reaction. It seems clear from Table 5 that feeding pigeons stimulate a very strong alighting response in passing birds and this habit seems so ingrained that it might be difficult for pigeons to feed as single individuals. Even a bird feeding alone might attract passing birds and defeat its individualistic behaviour.

The birds in a feeding flock normally all move in the same direction, which is into the wind. For some further observations, we arbitrarily divided the flock into three sections. We defined the front of a flock as the leading edge to the direction of movement. Often it was possible to see a single or a few individuals clearly in front of the flock but if this was not the case only those in the leading two ranks were defined as being in the front. This meant that no more than 10% of the flock was included and usually much less. The same rules were followed for those birds in the rear and the birds eligible for inclusion always represented a very small proportion of those present (always under 10%). All other birds were defined as being in the middle. This included birds on the side edges but as these were not always readily distinguished if a flock was seen at a distance moving at right angles to the observer, this was unavoidable. Flocks varied in shape from circles to



elongated ovals but had the birds been in a race the first over the line would have comprised the front individuals, the mass the middle and the last 10% or less the rear.

Table 5 also shows that those wood-pigeons joining a feeding flock were limited in the positions they selected, the middle of the flock being noticeably avoided. The behaviour seemed less marked when large flocks were involved but even so the proportionate area available in the centre of a large flock (over 80% by definition) greatly exceeded the edge area and the birds' distribution was not therefore according to expectation. Very large flocks could sometimes be considered as an aggregation of several small flocks and field observation suggested that the pigeons reacted towards small sub-units within the main flock in the same way as they did with smaller isolated flocks.

Those birds leaving a feeding flock were also much more liable to originate from the front or rear and rarely from the middle (Table 6). Judged by the figures in Table 6 for

Table 6. *The place of origin within a feeding flock of those wood-pigeons which flew*

Size of feeding flock	No. of flocks observed	No. of wood-pigeons leaving the feeding flock	Percentage leaving from the:		
			Rear	Middle	Front
1-20	4	254	40	9	51
21-100	7	712	33	8	59
101-150	3	332	33	36	31
Total and mean	14	1298	35	15	50

25% of the birds flying from the rear and 26% from the middle settled again in the flock, whereas only 11% of those leaving from the front settled again.

flocks of 101-150 there was no difference between the middle and front or rear, but as by definition the centre of the flock contained more than 80% of the feeding birds the distribution of departures was not in accordance with expectation. Again there is the consideration that large flocks were aggregations of many smaller ones.

### (b) *Feeding behaviour*

There were considerable differences in the feeding rate as judged by the number of food items collected (pecks) per unit time (minute) depending on flock position (Table 7). Abortive pecks do not occur frequently enough to nullify the assumption that pecks represent food items eaten. Birds in front of the flock took far fewer pecks (collected fewer food items) than those in the middle or rear. There was no difference in searching rate as evidenced by the number of paces per minute depending on flock position, hence front birds did not become isolated from the main flock. (When searching at high speeds as on grain sowings pigeon flocks are more dispersed but it seems that all the birds behave in the same way.)

Birds in front of the flock appeared uneasy in their feeding behaviour and continually looked up to see if other individuals were nearby. On one occasion two such individuals continued to feed when the rest of the flock departed for their roost at dusk, and furthermore their feeding rate increased.

Whenever a group of feeding birds was watched the front members seemed more uneasy and almost invariably had a lower intake rate. In Table 7, in fifteen out of nineteen cases

the front birds had lower feeding rates than those in the middle and in three of the four exceptional cases the feeding rates in the front were lower than at the rear. We are convinced that this lower feeding rate resulted because the leading birds spent more time watching and avoiding other birds, and we have numerous observations in which leading birds moved out of the way of those coming up from behind. On 12 March, twelve pigeons were feeding in a rough line on field 215. The average pecks per minute in order for each bird beginning with the front individual were: 76, 80, 88, 104, 114, 127, 104, 126, 132, 118 and 125 for the rear bird. The average paces per minute were 25, 27, 25, 25, 30, 14, 24, 29, 13, 20, 32 and 18.

These observations led us to suspect that submissive birds could be found at the front

Table 7. *The rate of food collection by wood-pigeons depending on their positions in the feeding flock*

Date	Field reference	Clover density per square foot	Position of birds in flock					
			Front		Middle		Rear	
			Average per minute of Paces	Average per minute of Pecks	Average per minute of Paces	Average per minute of Pecks	Average per minute of Paces	Average per minute of Pecks
16 Dec. 1965	244	356	11	71	14	79	12	89
5 Jan. 1965	244	356	19	88	22	94	23	99
7 Jan. 1965	244	356	20	110	23	108	19	115
17 Feb. 1964	4	224	37	74	14	126	16	122
11 Feb. 1964	4A	188	41	72	31	95	23	114
23 March 1965	221	184	40	107	38	99	38	107
17 Feb. 1965	221	140	21	120	21	136	24	131
11 Jan. 1965	F3	130	28	80	16	97	24	97
14 Feb. 1964	4C	123	19	71	32	67	38	74
14 Feb. 1964	211	95	20	70	24	75	24	78
27 Feb. 1964	211	95	44	80	28	105	38	98
27 Jan. 1965	66	92	33	86	25	106	30	98
18 Feb. 1965	9A	75	30	81	22	101	29	100
19 Feb. 1964	20	74	32	77	25	100	19	103
14 Feb. 1964	20	61	35	75	30	75	20	87
4 March 1964	66	59	32	89	35	107	24	115
3 March 1964	20	49	31	83	36	93	24	114
18 Feb. 1965	13A	24	48	65	33	79	38	80
4 March 1964	107	19	26	63	28	67	22	77
Means			30	82	26	95	26	100

The difference in mean pecking rate between the front and middle is significant ( $t = 2.360$ ), between front and rear ( $t = 3.451$ ) but not between middle and rear ( $t = 0.830$ ). There are no significant differences in the mean number of paces and in all cases  $n = 36$ .

of the flock whereas before we had assumed, rather anthropomorphically, that these birds were the 'leaders'. The existence of a social hierarchy in the feeding flocks was now suspected and it became necessary to establish whether the position adopted by birds within the flock was fluid or relatively static. In 1964 in three separate cases where observation was possible the same individual stayed in front of the other feeding birds for about 2 h at which point the flocks were flushed, or disturbed. The impression was strong that birds kept to the same position relative to other individuals for long periods.

### (c) *Social hierarchy*

It is extremely difficult to demonstrate the existence of any hierarchy unless a large proportion of the birds in a flock are recognizable as individuals. Moreover, there is little

obvious indication in a feeding flock of pigeons that intra-specific competition occurs. For example, in the winter of 1962–63 we watched on different occasions fifteen flocks on clover sites averaging fifty-one birds (range 3–238) for a total time of 136 min and saw a total of twelve aggressive incidents involving supplanting attacks. There was no indication that conflict situations were related to food density or flock size and the general incidence of this kind of behaviour was low compared with that seen in feeding flocks of some species, for example rook (*Corvus frugilegus*) or starling (*Sturnus vulgaris*), or even with pigeons when snow covered their feeding grounds (Murton & Isaacson 1962). However, a clear social hierarchy has been demonstrated in *C. livia* under domestic conditions (Masure & Allee 1934). Nevertheless, when a flock of feeding pigeons was carefully

Table 8. *Sightings and flock position of albino wood-pigeon in winter 1964–65*

Date	Time (hours)	No pigeons feeding	Position or range of position of albino counting from flock front	Remarks
18 December	10.45	154	143	To rear and right of centre of flock
21 December	12.30–13.30	252	159–170	To rear and right of centre of flock
22 December	14.00–15.15	220–286	27–122	Near front when first seen but then dropped to rear position as above
11 January	14.10	142		Albino not present but arrived with another bird at 14.10 hours and settled in position 25
	14.20	144	80	Albino let other birds pass until it reached rear of flock
	14.30	144	98	
12 January	10.00–11.54	190	65–86	For 2 h the flock stayed constant and the albino averaged position 76 (nineteen observations)
	11.54	190	189	Flock flushed to far side of field and albino sat down
	12.00–12.15	190	181–160	Stood and moved forward in flock
13 January	09.45	441	220	To rear and right of centre of flock
	14.00	235	99	
14 January	10.45	400	253	
19 January	13.13–13.25	195	100	
1 February	14.58	190	159	Flock flushed across field and albino settled approximately in the same position
	15.00	190	155	
3 February	11.15–12.00	95	70–92	Usually on rear right edge

All records refer to one field, No. 244.

watched it became apparent that a kind of hierarchy does exist. A bird feeding in the proximity of others might turn and feed towards another bird which immediately turned slightly to avoid the first. Often these supplanting attacks were very subtle and it was difficult to be sure whether a movement arose because a bird first moved towards another or whether a movement away created a vacant place. Records are accumulating from work on marked birds now in progress to show that these individuals do keep to approximately the same position in the flock throughout the day and on subsequent days. Particularly striking was the example of a readily distinguishable albino which was present in 1965 and which was invariably found in association with the flock inhabiting field 244. Details of sightings and of its position in the flock judged by the number of birds from it to the front of the flock are given in Table 8. While some objective method has to be used for defining the position occupied by a bird it is clear that an individual could live say on the right-hand rear edge of a flock of fifty and still be in approximately

this same position when 500 birds were present. Its position by number from the front sides or rear of the flock would not then be a full description. Sketches of the flocks were made and in the case of the albino it was noticeable that the bird was always seen near the rear left edge.

A bird with an orange wing disk was feeding in position 2 in a feeding flock of seventy birds on field 107 at 11.15 hours on 19 January 1965. The front five birds were all well separated from the main concentration of birds. At 11.23 hours another thirty-six birds arrived and some reshuffling occurred up to 11.45 hours so that 'orange disk' dropped back to position 52. At 11.45 hours it then flew forward to occupy a front position and stayed there until the flock was flushed at 12.00 hours.

On 24 March 1965 wood-pigeons 59 and 68 were located at 15.05 hours feeding in an elliptical flock of sixty-three birds on field 4B. Both birds occupied rear positions (in fifty-third and forty-seventh position respectively) with 59 on the rear left edge and 68 more central and separated from 59 by two unmarked birds. At 15.20 and 15.30 hours when checks were made the birds were still in the same position. At 15.35 hours the whole flock was flushed and flew to the far side of the field. When the flock landed eight unmarked birds immediately rose from the front and resettled in the flock centre. At 15.40 hours 59 and 68 were in the same position in the flock (fifty-four and fifty-one birds back from the front) with 59 on the rear right edge and 68 more central separated by two unmarked birds.

It is noticeable that a feeding flock moves gradually across a clover field and that few flights or changes in position are seen. If the flock is disturbed and it resettles it is most noticeable that for the next 5 min or so there are numerous movements and flights back and forth as the birds interchange positions. Such behaviour and the other observations quoted seem strong evidence that a stable flock structure exists and while more evidence is desirable it seems reasonably safe to assume that in general each bird maintains its own position relative to the others.

Flocks certainly inhabit the same field or group of fields for long periods and there is normally little interchange of birds between flocks in the absence of disturbance. Apart from subjective impressions and the inferences that might be drawn from Table 8 (if the albino was conservative in its choice of feeding ground so presumably were its flock-mates) the marking and recapture of birds during experiments with stupefying baits provides further evidence (see Murton, Isaacson & Westwood (1963b) for some earlier data). Another example was an experiment begun on a clover-ley at Fordham (about 20 miles from Carlton) on 14 January 1965; of forty-two birds ringed and released and available for further capture, ten were seen or caught again on the same field once, five were recorded again twice, two on three occasions, two on four occasions and one was seen and caught five times (total of twenty different birds). Observations and recaptures extended to 24 February. Eighteen of the birds were released at Carlton and two returned to their original feeding ground at Fordham, a distance of 11 miles, one within 12 days and one within 2 days. This homing ability has been noted in other work of this sort (in progress).

It seems, therefore, that a few individuals at the front of the flock have low feeding rates and that this situation continues over long enough periods for the cumulative effects to be significant (see below). It is highly probable that flock stability is such that birds experiencing low feeding rates would do so day after day. A true social hierarchy might imply that pigeons are able to recognize each other as individuals, but whether or not this is the case is not known. It need not be a necessary requisite and the above results could be achieved if each pigeon adopted a position in the flock where it felt most at ease.

(d) *Feeding rates and clover density*

It has already been shown (Murton *et al.* 1963a) that on grain stubbles and wheat and barley sowings the speed of food collection by wood-pigeons is a function of searching rate, as measured by the number of paces taken per minute and food density or the number of grains per square foot. As food density fell the birds compensated by increasing

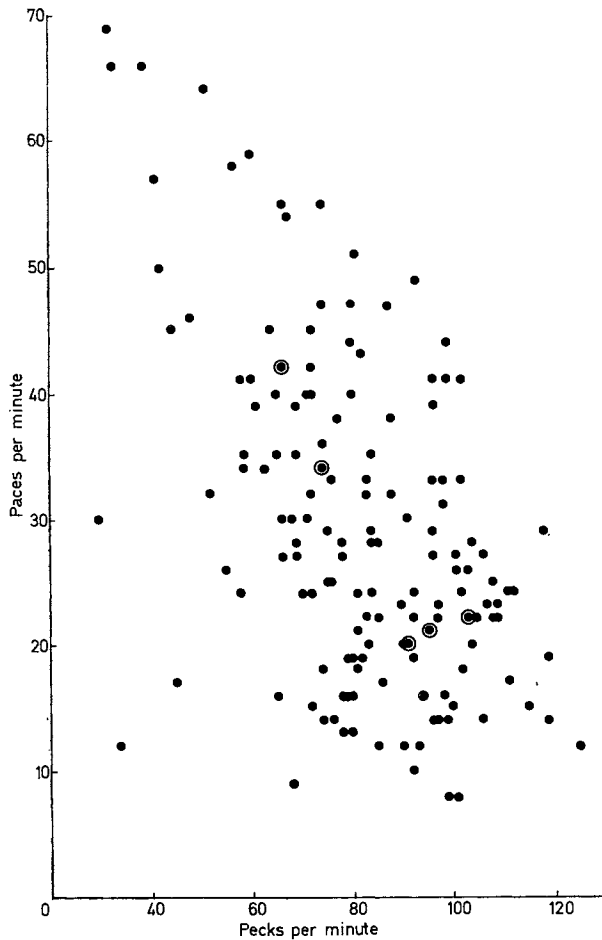


FIG. 6. Relation between number of pecks and number of paces taken per minute when clover density remained constant. Each dot represents the reading for a different wood-pigeon. Data collected on a pasture on 26 February 1960.  $r_{151} = -0.510$ . Regression formula:  $y = -0.753x + 103.918$ ;  $x = -0.345y + 57.528$ .

their speed of food searching until a critical point was reached at which they could no longer search quickly enough to pick up sufficient food. With an increase in food density the birds eventually reached a point at which they maintained a constant search rate irrespective of food density.

The information in Table 7 does not indicate any relationship between clover density and searching or feeding rates. But the observations were made at all times of day and this may have confused the situation because it is known that the feeding rate on pastures varies considerably throughout the day (Murton *et al.* 1963a). On the same pasture in

1960 mean pecking rate varied between 64 and 102/min throughout the day and the mean paces per minute between 26 and 35. In Table 7 the reading for field 244 on 16 December was taken at 10.40 hours, that for 5 January was taken at 12.00 hours and that for the 7 January at 14.00 hours and wide variations are apparent.

All available observations of feeding rates at known clover densities are given in Table 9 (for many of these observations the flock position of the birds was not considered and so the figures represent the rough average for the whole flock). More paces were made per minute with decreasing clover density for observations between 10.00 and 12.00 hours

Table 9. *The feeding rates of wood-pigeons in relation to clover density*

Observations made 10.00–12.00 hours				Observations made 13.00–14.00 hours			
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Clover density	No. birds timed	No. per minute of Paces	Pecks	Clover density	No. birds timed	No. per minute of Paces	Pecks
893	10	13	90	662	10	21	78
439	10	18	91	363	10	31	85
365	10	29	78	356	5	23	108
356	8	14	79	280	7	44	86
356	5	22	94	245	10	38	94
280	3	9	81	233	8	29	66
229	9	27	61	188	4	31	95
152	5	19	75	185	11	24	92
152	5	21	82	184	5	38	99
130	5	16	87	152	4	31	82
95	4	24	75	152	5	17	80
92	5	25	106	140	5	21	137
75	5	22	101	123	5	32	67
74	5	25	100	95	5	28	105
61	5	30	75	68	10	31	70
35	8	36	56	63	11	32	71
33	10	31	55	59	10	42	85
24	5	33	79	59	5	35	107
19	5	28	67	49	5	36	93
				31	5	34	65
Means		23	81			31	88

The correlation coefficients between columns are: 1 and 3  $r_{17} = -0.594$  (significant)  
 5 and 7  $r_{18} = -0.329$  (not significant)  
 1 and 4  $r_{17} = 0.237$  (not significant)  
 5 and 8  $r_{18} = 0.007$  (not significant)

for columns 1 and 3 the regression formula is:  $y = -0.020x + 27.341$   
 $x = -17.563y + 611.732$

( $P = 0.01-0.001$ ) but not for observations made in the period 13.00–14.00 hours. At no time was the pecking rate related to clover density, although it did appear to decline at very low clover densities (see below).

Fig. 6 is based on feeding rate observations made on a single pasture between 08.50 and 1550 hours on 19 February 1960 and shows that there was a very strong negative correlation ( $r_{151} = -0.510$ ,  $P > 0.001$ ) between the searching and feeding rate when clover density remained constant. An increased intake rate had to be at the expense of the area searched for food. It is known that wood-pigeons take more pecks relative to their searching area towards late afternoon and it has been suggested that they are less selective in what they collect especially as at this time some food is being stored in their crops for later ingestion

at the roost (Murton *et al.* 1963a). It is conceivable that any tendency to be less selective would remove the need to relate to food density the area searched per minute. Although Table 9 shows an increase in the area searched in the afternoon it should be noted that a different sample of clover densities was considered and as it has been established that there is a relation between clover density and paces this does not contradict the above statement.

A wood-pigeon's pace averages 4.2 in. and from Table 9 it is easy to calculate that in moving one foot the birds took between nine and eleven pecks. They can probably reach an area of about 4 in. on either side and can see ground objects from 6 to 12 in. on either side. Hence, they were effectively searching about three-quarters of a square foot with every three paces, and it is clear that, except at the lowest clover densities, the number of leaves taken relative to those present was quite low. As mentioned, it is the general experience of workers concerned with grazing behaviour that animals tend to be selective in the food they take (see references given on page 56). It is conceivable that the pigeons were also selective, for instance, they might have preferred the young more nutritive clover leaves or those most easily picked. If selection was the rule it is obvious that for every three paces at clover densities of about 100 leaves/ft<sup>2</sup> the birds would have to collect about ten leaves out of seventy-five, a fair choice, but at a clover density of say 50 leaves/ft<sup>2</sup>, ten leaves out of only thirty-eight, a proportionately much worse choice. If leaf selection is at all important in the nutrition of wood-pigeons, fields with clover densities of say less than 50/ft<sup>2</sup> might be poor or unsuitable as feeding grounds. If selection is unimportant it is difficult to see why the birds' feeding rates in the morning should not resemble those of the afternoon.

For a more critical analysis of the effects of clover density on feeding rates those data which were collected at comparable times (most information was available for the 10.00–12.00 hours period) and where the flock position was also known are plotted in Fig. 7. Each dot gives the mean pecking rate per minute for different individuals, and the mean values at each clover density for all individuals are also shown. Significant correlations (see caption to the figure) were found showing that pecking rates decreased when clover densities of less than 100 leaves/ft<sup>2</sup> were considered although the number of paces taken was not affected (not shown). As over a wider range of clover values the searching rate did vary with density it might be suspected that at these low values the number of paces was a maximum compromise consistent with collecting a reasonable supply of food. The activity and the physiological demands that must be involved in taking around one pace and two to three pecking and swallowing movements every 2 sec can perhaps be imagined.

Murton *et al.* (1963a) showed from many observations that the mean pecking rate on pastures in February throughout the day was 81/min although it started in the low 70s in the morning and reached 103 in the afternoon, and the birds took a little more than 30 000 fragments of clover plus some incidental grass and weed leaves, in an 8-h feeding day. The average rate between 10.00 and 12.00 hours in February was 74/min. The daily average figure of eighty-one compares reasonably with the average figures given in Tables 7 and 9. But to maintain this average against low morning rates it would normally be expected to find pecking rates a little in excess of a hundred in the afternoon. In Table 7 figures above a hundred pecks per minute were noted for middle and rear birds at clover densities down to 49/ft<sup>2</sup>, whereas no such values occurred for front birds until clover densities of 140/ft<sup>2</sup> were experienced. Though subject to sampling errors this does suggest that a critical stage could be reached when front birds would get insufficient food, although the rest of the flock would be able to feed satisfactorily. On average front birds

obtained 14% less food than middle birds, and it can be inferred from Table 7 that this percentage difference was constant irrespective of food density. Considering the data in Fig. 7 it might be suspected that below clover densities of 50/ft<sup>2</sup> front birds would get

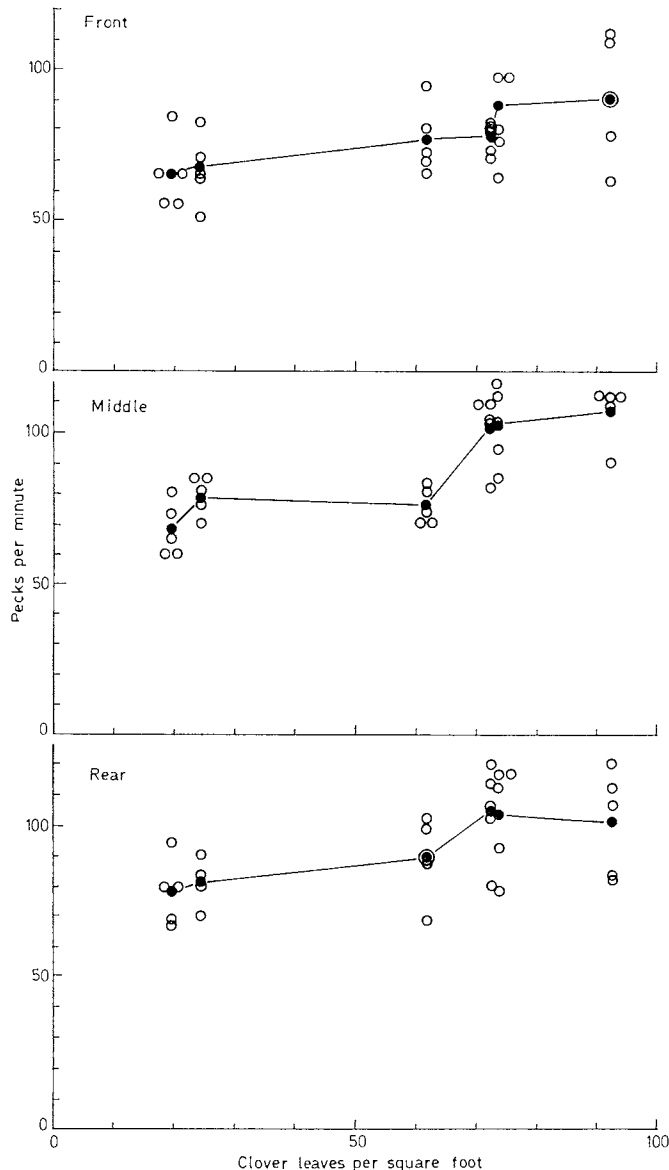


FIG. 7. The number of pecks taken per minute by wood-pigeons when feeding on pastures with low clover densities. Each dot represents the observations for a different bird and the curves are drawn through the means. Correlation coefficients for clover density against pecks: Front,  $r_{28} = 0.579$ ; middle,  $r_{28} = 0.762$ ; rear,  $r_{28} = 0.599$ .

insufficient food and the effect might operate at higher clover densities if active food selection is important in modifying the nutritional value of the birds' total food intake. Thus in Fig. 7 the front birds had feeding rates of sixty-six instead of at least seventy-four and there is no doubt that such a difference would have profound cumulative effects. Thus



if any mortality caused by food shortage occurred it could be restricted to relatively few individuals.

## 5. THE EFFECT OF CLOVER AVAILABILITY ON WOOD-PIGEON NUMBERS

Although any reductions in clover availability that result from the wood-pigeon's feeding behaviour are transient and the plants recover uninfluenced by defoliation, the wood-pigeon population suffers for a much longer period. Murton *et al.* (1964a), supplemented by Murton (1965a), have shown that the minimum size of the winter wood-pigeon population in the study area was determined by the lowest level to which the clover stocks decreased.

Opponents of the view that direct competition for food resources can provide the main factor regulating bird populations often raise the point that starving individuals are rarely encountered. It was Lockie (1956) who pointed out that in rooks the bulk of the birds in a population remained at normal weight and that only a few individuals could be found starving at any one time. Similarly a low mean weight of wood-pigeons in winter reflects the condition of a few individuals and not all the birds. This situation can be seen in Fig. 8 where the weights of wood-pigeons shot coming to roost in February in different years are arranged in frequency classes. Except in 1963 there was always a clearly defined peak containing most of the population and only a small but variable proportion could be defined as being under-weight.

In winter wood-pigeons average 500 g and we have arbitrarily considered that a bird weighing less than 450 g would be in poor condition. It seems reasonable to suppose that such birds would most likely die under adverse conditions and that the size of the low weight classes would indicate the proportion of the population in the process of starvation. Adults and juveniles have been considered together because from a population point of view the weakest birds would be lost and it matters not at the moment whether they were adults or young. The proportion of 'under-weight' birds in the population is given in Table 10 and it can be seen to bear little relationship to clover availability. On the other hand the proportion of 'starving' birds bears a clear relationship to the mortality or survival rate as judged by the difference between population size at the beginning of winter and the loss (or gain in numbers) to February. Thus the amount of food available *per se* was unimportant in determining body condition and it was the number of birds in relation to food stocks that determined whether starving birds were found. Although this seems reasonable and to be expected there is little other field evidence available on the subject. In 1961, the clover food supply was very high and the population supportable by February was also high. Yet pigeon numbers were extremely high at the end of the previous autumn (because grain supplies—the autumn food—had been good) and considerable mortality had to occur. There was evidence that many birds were starving. In contrast 1963–64 was a winter of very poor clover supplies but the population started off in balance with food stocks and little mortality occurred and as a consequence few birds appeared to be starving.

Another indication that mortality was the result of starvation is given by the amount of food in the crops of birds returning to roost. All the birds detailed in Table 10 were shot under the same conditions at a time when they should have had food in their crops—in fact their crops should have been full (Murton *et al.* 1963a). If some pigeons are prevented from obtaining sufficient food through competition within the feeding flocks (Section 4) then it might be expected that they would return to their roosts with less food

than other birds. It was, therefore, assumed that the proportion of birds judged to have virtually empty crops (this could be ascertained by feel without spoiling the market value of the birds) indicated the level of under-feeding in the population. Table 10 shows that a high proportion of birds with empty crops was found in those years with a high proportion of under-weight birds and a high mortality rate. When feeding on clover the average weight of a full crop is around 43 g and the absence of crop food could not be held as the sole cause of a high proportion of birds having low body weights in certain years.

If wood-pigeons were able to reduce their food stocks below an optimal subsistence level before competition occurred it is clear that the whole population would be affected

Table 10. *Relationship between wood-pigeon body weight and mortality in relation to clover food supply*

Age class	No. birds examined	Mean weight $\pm$ SD (g)	% under 450 g	% birds with empty crops	Population per 100 ac in December (maximum)	Lowest level reached by population in February or March per 100 ac	Difference (%)	Clover index in February
1959								
Adult	26	542 $\pm$ 34	} 2	2	117	97	-17	
Juvenile	18	511 $\pm$ 35						
1960								
Adult	79	476 $\pm$ 51	} 25	Un-known	62	34	-45	1338*
Juvenile	6	(433) $\pm$ 49						
1961								
Adult	29	509 $\pm$ 62	} 19	29	174	83	-52	1887
Juvenile	23	472 $\pm$ 38						
1962								
Adult	153	536 $\pm$ 40	} 5	5	51	64	+25	1676
Juvenile	21	485 $\pm$ 41						
1963								
Adult	44	499 $\pm$ 76	} 36	39	104	1	-99	0
Juvenile	18	442 $\pm$ 59						
1964								
Adult	38	560 $\pm$ 63	} 14	3	41	33	-20	1132
Juvenile	36	488 $\pm$ 47						

Data refer to birds shot coming to roost at dusk in February.

\* Refers to early March.

and all individuals would suffer a decrease in body weight. The observations, therefore, imply that competition was occurring in such a way that only a few birds starved at one time and by inference died as the population was continuously adjusted to the available food resources. The hard winter of 1962-63, when snow covered all clover feeding grounds from late December until early March, was an exception and pigeons were forced to move on to *Brassicae*. The amount of *Brassica* leaf that has to be consumed compared with clover is higher because the water content may be around 86% compared with 80% or less for clover and further the digestible crude protein content can be half that of the equivalent dry weight of clover. It has been our experience that when wood-pigeons have to subsist entirely on *Brassica* leaves they lose weight and are in poor condition. To some extent the effect of feeding on *Brassicae* might be comparable with one in which clover stocks were reduced below the critical level for efficient feeding, a situation that would

follow from the breakdown of competition mechanisms. Fig. 8 shows that when the birds were all forced to feed on *Brassicae* many more suffered; the proportion of under-weight birds was increased and that of the middle-weight class decreased.

The age classes in Table 10 should have been sampled in true proportion to their distribution in the population; the subject of differential survival rates between adults and young over the autumn has already been discussed (Murton *et al.* 1964a; Murton 1965a). It can be seen from Table 10 that in February first-year birds had a lower mean weight than adults; it might be presumed therefore that they would be the first individuals to appear in the very low weight classes in adverse conditions and that they

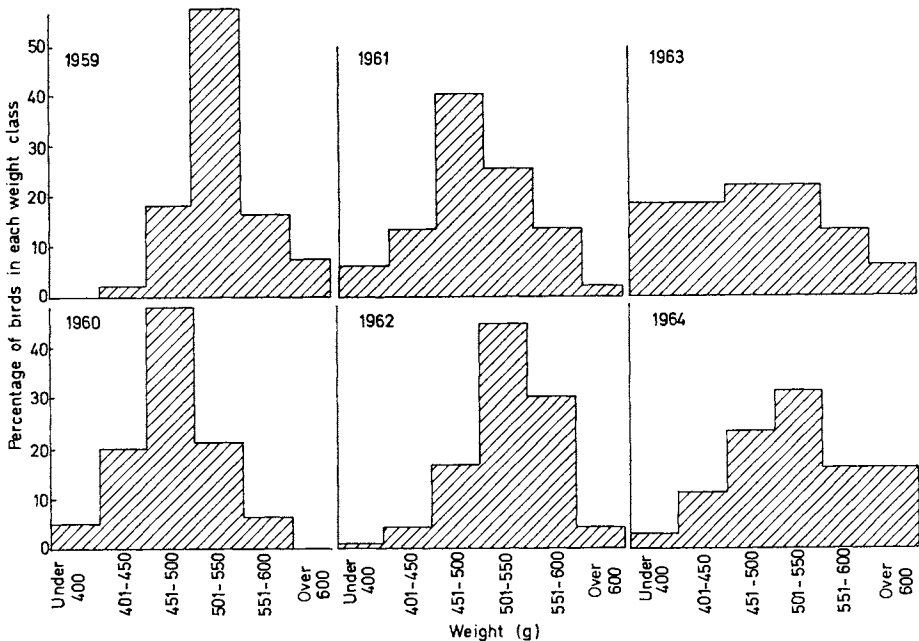


FIG. 8. The percentage number of shot wood-pigeons in various weight classes in different years. 1959, mean 529 g, 44 birds; 1960, mean 473 g, 85 birds; 1961, mean 492 g, 52 birds; 1962, mean 530 g, 174 birds; 1963, mean 482 g, 62 birds; 1964, mean 525 g, 74 birds.

would also suffer a higher mortality. The samples are not really large enough to show this but some additional figures are presented in Table 11. These birds were caught with stupefying baits and when weighed usually had empty crops, whereas most birds in the shot sample had full crops, but the trends in weight distribution follow those detailed in Table 10. Three facts can be gleaned from the table. First, the mean weight of wood-pigeons was lowest in February when there were more birds in the low weight categories, indicating that this could be the month when the pigeons experienced the greatest mortality. Further evidence for 1961 can be inferred from the fact that forty-one adults shot in March averaged 522 g ( $SD \pm 44$  g) which was more than those shot in February, while Table 11 shows that mean weight was higher in January. Second, in those years when sufficient young were available for collection, they contributed proportionately more individuals to the lower weight classes than did adults. Whereas adults always decreased in weight from January to February, first-year birds increased. This might be attributed to growth but may have been due to a higher mortality rate of young in

Table 11. *Weight distribution of wood-pigeons caught with stupefying baits*

Date	Age class	No. of birds in weight category						Over 600 g	Total birds	Mean weight $\pm$ SD (g)	% under 450 g
		Under 400 g	401-450 g	451-500 g	501-550 g	551-600 g	600 g				
1960	Adult	2	14	25	10	2	0	53	470 $\pm$ 43	30	
	Juvenile	1	1	1	0	0	0	3	(400)	(67)	
	Adult	4	6	12	3	0	0	25	455 $\pm$ 48	40	
	Juvenile	3	3	3	0	0	0	9	406 $\pm$ 64	(67)	
	Adult	5	18	35	23	5	2	88	479 $\pm$ 57	26	
	Juvenile	2	3	4	2	1	0	12	458 $\pm$ 63	(42)	
1961	Adult	2	13	30	37	18	1	101	503 $\pm$ 49	15	
	Juvenile	19	23	22	12	4	0	80	443 $\pm$ 64	53	
	Adult	1	14	20	9	7	2	53	487 $\pm$ 55	28	
	Juvenile	5	9	7	2	2	0	25	445 $\pm$ 61	56	
	Adult	0	2	7	28	14	2	53	534 $\pm$ 40	4	
	Juvenile	5	9	14	13	2	0	43	472 $\pm$ 52	33	
1964	Adult	0	7	12	46	27	7	99	533 $\pm$ 48	7	
	Juvenile	4	23	36	31	6	2	102	486 $\pm$ 54	26	
	Adult	0	2	9	15	13	2	41	537 $\pm$ 44	5	
	Juvenile	2	10	14	9	4	0	39	481 $\pm$ 54	31	

January so that as the lightest individuals died, the mean weights of the remainder increased. We have already shown that juveniles suffer a higher shooting mortality early in the winter but this approached the adult level sometime in February, at which time first-year birds are no easier to shoot than adults. Nevertheless, they are probably at greater risk of dying from starvation in the face of competition from the adults; experience and fitness for one aspect of survival need not confer any advantage for other subsistence requirements. Third, it can be seen from the table that some birds were underweight in all three months and not just at those times when food supplies reached a minimum so that population adjustment could have been a continuous process.

In 1960 when the mortality rate was high (Table 10) there were many birds in the low weight classes throughout January to March. In that year there were few juveniles in the population and it was mainly adults that suffered. In 1961, the total mortality rate was even higher but because a large number of young were available in the population they were the main contributors to the low weight classes. In 1964, overall mortality was rather low and it was again the first-year birds that apparently suffered most. Thus it seems that adults are always favoured whatever the conditions.

Wood-pigeons may lose weight very rapidly under adverse conditions. In a few cases we have captured individual pigeons with stupefying bait on several days in succession and their feeding was consequently disturbed. One bird caught on three occasions weighed 463 g on 8 January 1961, 400 g when caught 3 days later and 332 g on the fifth day (normally we feed captured birds before release to prevent such weight loss). Another bird decreased from 446 to 385 g in 3 days. Conversely pigeons may increase rapidly in weight. Thus one bird weighed 415 when first caught in January but it weighed 448 g 3 days later; on each occasion it had an empty crop. Further information is given in Fig. 9 for some birds caught in recent trials.

Though small numbers of pigeons can be lost from the population as a continuous process the chances of finding dead bodies must be very small indeed, because scavengers like the rat (*Rattus norvegicus*) and fox may very rapidly remove dead bodies. We have many records in which a carcass purposely left on the ground vanished overnight, often without trace. That dead birds are rarely found does not disprove the contention that birds die of starvation. In fact, the usual level of pigeon mortality experienced at Carlton would require no more than one bird to die per 100 ac per day. Some of these birds are shot before natural death overtakes them, and some may emigrate, but even in the absence of shooting or emigration this scale of mortality could be easily overlooked. Ailing birds usually seek shelter in which to die and it is our impression that most die in the roosts at night. In unusual circumstances when a lot of birds die at the same time bodies are found. This was the case in 1961 when pigeons were poisoned by organochlorine insecticides used on spring cereals and in the hard winter of 1962–63. In such cases sudden death often overtakes birds when away from shelter.

In 1960 and 1961 the clover density was not measured on those fields where stupefying baits were laid. In 1962 and 1963 trials were done outside the study area on only two clover sites of high density and again in 1964 most work was done on field 211 with a high clover density. However, in 1965 of three trials undertaken at roughly comparable times two were on areas of high clover density (similar to earlier trials) and one was on field 215 which had a very low clover density. The weight details given in Table 13 for birds caught during these three trials, therefore, refer to individuals belonging to three separate flocks. It is apparent that the mean weight of birds varied considerably between flocks and that it was low on field 215. Considering all the evidence given in this paper

Table 12. *Weight distribution of wood-pigeons from three separate flocks in 1965. Birds caught with stupefying baits*

Trial reference and dates of study	Location	Age class of birds	Under 400 g	No. of birds in weight category				Total birds	Mean weight $\pm$ SD (g)	Clover density per square foot (No. samples in parentheses)
				401-450 g	451-500 g	501-550 g	551-600 g			
4 28 January to 18 February	Fordham	Adult	2	5	8	5	1	21	470 $\pm$ 47	217 (10) on 15 January
		Juvenile	10	23	12	2	0	47	429 $\pm$ 39	139 (10) on 5 February
8 24 February to 30 March	Field 215	Adult	5	24	14	3	1	47	440 $\pm$ 44	35 (10) on 23 February
		Juvenile	3	4	2	0	0	9	411 $\pm$ 42	54 (10) on 12 March
6 5 February to 18 February	Field 221	Adult	2	5	9	1	0	17	457 $\pm$ 35	146 (10) on 2 February
		Juvenile	3	2	0	0	0	5	401 $\pm$ 27	140 (6) on 17 February 184 (6) on 16 March

The differences in mean adult weight between birds from trials 8 and 4 are significant ( $t_{66} = 2.542$ ) but not between trials 8 and 6 ( $t_{62} = 1.44$ ).

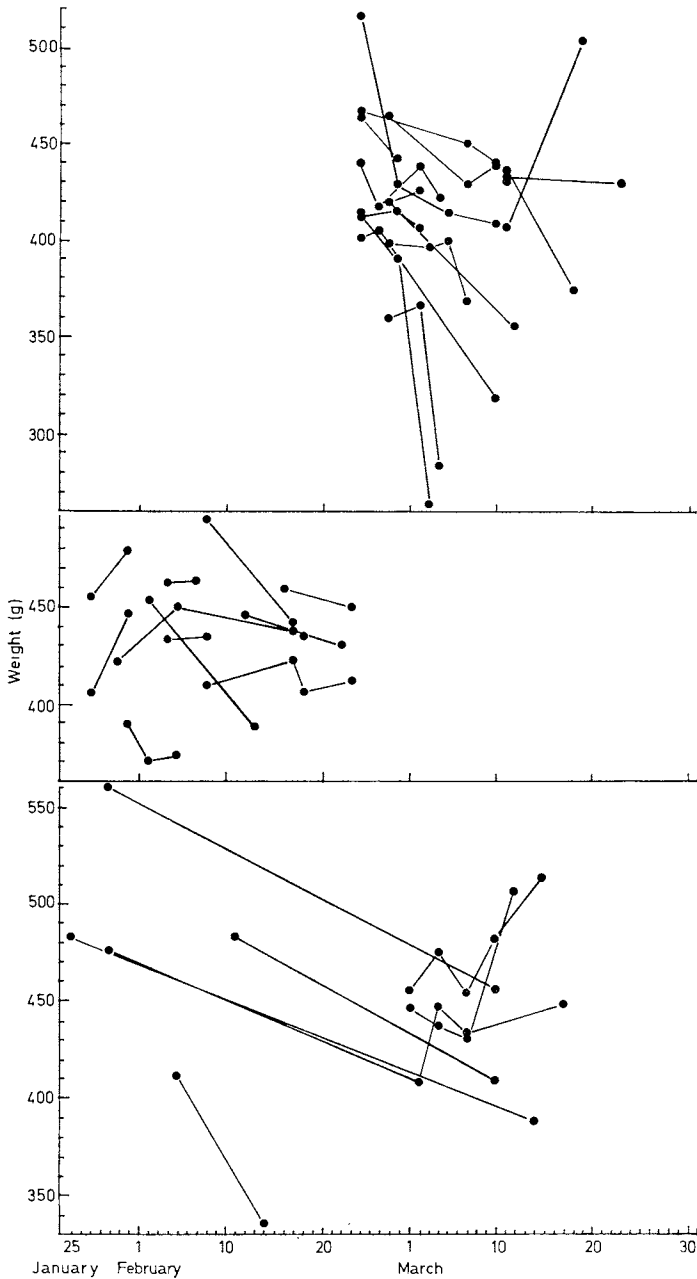


FIG. 9. Variations in body weight of stupefied wood-pigeons from different flocks that were caught more than once using baits treated with alpha-chloralose. Top—caught during experiment 8 on field 215 in 1965. Middle—caught during experiment 4 at Fordham in 1965. Bottom—caught on a pasture in 1960. Clover density was exceptionally low on field 215, but see text for discussion and also Table 12.

it seems reasonable to attribute this low weight to the poor feeding conditions and to postulate that the mortality in this flock was higher than elsewhere. Particularly striking was the sharp decrease in weight of birds captured on more than one occasion compared with the loss of weight of birds caught during experiment 4 (Fig. 9). Insufficient information was available for experiment 6 but details are given of a trial done on a high clover density pasture in 1960 over a comparable period.

Kluyver (1957) found that male great tits (*Parus major*) were usually dominant over females and as a result were more successful in obtaining roosting sites. It seemed

Table 13. *Sex ratio of wood-pigeons in different years*

		No. adults		No. juveniles		% of males (adults and juveniles combined)
		Males	Females	Males	Females	
1959	February	4	5	3	1	
	March	4	5	2	5	
	Total	8	10	5	6	45
1960	January	33	26	10	9	
	February	73	65	8	6	
	March	31	26	3	5	
	Total	137	117	21	20	54
1961	January	15	17	13	20	
	February	33	49	38	32	
	March	48	51	20	12	
	Total	96	117	71	64	48
1962	January	43	35	22	17	
	February	9	11	2	1	
	March					
	Total	52	46	24	18	54
1963	January	13	15	} Adults and juveniles combined		
	February	11	15			
	March	13	13			
	Total	37	43			
1964	January	43	34	22	19	46
	February	44	51	45	48	
	March	32	31	28	34	
	Total	119	116	95	101	50
Total without 1963		412	406	216	209	51

possible that male wood-pigeons would be dominant over females and as a result the females might be the first birds to leave a feeding flock at times of social pressure. It might be expected that survival in females would be lower than in males so that their ratio in the population would be low in years of high winter mortality. That this was not the case is shown in Table 13 where information from birds shot or captured with stupefying baits is presented. The proportion of males and females in the population did vary in different years, for reasons at present unknown, but at no time was there any suggestion that a high proportion of males was correlated with a high mortality rate as judged by the figures in Table 10.

## 6. A DISCUSSION OF THE MECHANISM OF POPULATION CONTROL

When clover stocks were lowest and wood-pigeon numbers had declined to a minimum level in parallel with changes in the food supply much clover apparently remained available. In 1964 in February when the lowest clover stocks recorded in any year were



experienced it can be calculated (knowing the average clover density per square foot, the acreage available and how much one pigeon eats per day) that there was enough clover left per 100 ac to last one pigeon for 2403 days or a population of thirty-three birds for 73 days. The birds seemed to have left themselves a very considerable safety margin, but it is possible that the area with clover densities sufficient to maintain an adequate feeding rate may have been limiting. Unfortunately our sampling methods were not detailed enough in 1960 and 1961 to evaluate the clover content in individual fields, although this could be done in 1962 and 1964 (in 1963 the fields were snowbound). Thus in 1964, 63% of all the clover acreage in February supported leaf densities below 100/ft<sup>2</sup> and 43% below 50/ft<sup>2</sup> (total acreage was 745). On pastures the average leaf density was only 85/ft<sup>2</sup> (72 ft<sup>2</sup> samples). It was noted above that at leaf densities below 50/ft<sup>2</sup> the pecking rate showed evidence of a decline that would make the collection of sufficient food impossible (Fig. 7). Considering these arguments, and allowing for errors in field observation, it might be that the birds fed much closer to the limits of their food supply than was at first apparent. Why should total population size be so clearly correlated with food stocks in different years if there did exist an unexploited reserve in each year?

(a) *A hypothesis for the mechanism of population control*

In Section 3(c) there is evidence that clover leaf survival was proportionately greater at low leaf densities during the first part of the winter (November to February) but that no such relationship occurred with clover densities of over about 150 leaves/ft<sup>2</sup> (Fig. 4). It was suggested that the absence of pigeon feeding at low clover densities could account for this result. Because more leaves were recognizable as having been eaten by pigeons where more leaves were available (Table 3), it must follow that either more birds fed or that each bird fed for a longer time where more clover was available. Table 4 shows that in January pigeons were avoiding fields with low clover densities, but not apparently in February (see below), while Fig. 5 suggests that the birds also sometimes distribute themselves according to food stocks in February.

Birds (animals) have presumably evolved some mechanism enabling them to relate searching effort to the amount of food found and certainly they can recognize a situation where no food exists and respond by searching elsewhere. Unfortunately it is not known in quantitative terms how long a pigeon requires to recognize and react to an unfavourable feeding situation. However, it is feasible that this could be a continuous process with the bird at all times being able to relate searching effort to food returns until a point was reached at which a very high searching rate necessitated flight. Conversely, it is possible that the feeding rate in turn affects what food is eaten and the possession of characteristic searching motor responses could determine within limits what food was selected by a particular species. In other words, a running bird would tend to find some objects more easily than others, whereas walking might enable it to locate those objects that were previously missed. The food eaten would then depend on what was available in a given environment at a suitable density to provide a feeding stimulus for a bird searching at a characteristic rate. Innate and learned food preferences could primarily determine what was eaten but it is perhaps undesirable to think of food collection only in terms of the animal searching specifically for what it requires. If this were so an animal could evolve the mechanism to respond to a threshold point below which the number of food items found per unit of searching time would be inadequate.

We now assume that pigeons which left from the front of the flock as was shown to happen in Section 4(a) did so because they were prevented from obtaining sufficient food

under the existing conditions. Birds which left from the rear may have obtained sufficient food and have been ready to return to roost or to rest in trees near the feeding grounds. However, whereas few birds which left the front of the flock tried to settle again (11%) a much higher proportion originating from the rear and middle did so (25–26%). Similarly it seems likely that pigeons arriving at the flock settle outside until their social position has been established; it would be expected that only a very dominant bird would choose to alight in the centre of a flock and so face immediate competition from established feeders. It therefore seems highly probable that front birds may leave a flock to search elsewhere if their intake of food is insufficient. But because the gregarious habit is so fixed this behaviour would result in the birds trying to join another feeding flock. Provided that surplus feeding grounds existed with high enough food densities it would be expected that neither flock distribution nor flock size would be related to clover density except that low clover densities should be avoided. A decrease in clover density should result in a loss of birds from some sites and the establishment of flocks at lower densities so that the birds might be distributed according to density as sometimes seems to happen. Further clover reductions could result in flocks being forced to feed at low clover densities and the birds' distribution might no longer match food availability, as in February in Table 4. But in such an event mortality through the starvation of some birds would be expected or alternatively emigration motivated by food shortage. If a flock was forced to feed at very low clover densities then all the birds should show evidence for a loss of condition and the same would happen if the flock exploited a less nutritive food source like *Brassica* leaves as happened in 1963. Summarized in Table 4 are data for three flocks inhabiting fields 244, 107 and 13A in February which were much bigger than would be expected on the basis of food availability. While the flock on field 244 could be explained by the limited availability of clover fields in that part of the study area it should nevertheless have shown signs of mortality. Unfortunately no data are available for these fields but some of the figures in Table 12 and Fig. 9 which refer to similar situations demonstrate that starvation could well have been occurring. It now seems highly feasible that in places like the study area most of the flocks could go through the winter on fields where clover stocks were never limiting and as a result little or no mortality would occur. But here and there one flock might be found where nearly all the mortality was taking place. The net result would be that total numbers would be related to total food at the worst season but that a detailed examination within the population would show little evidence of loss. Thus in Table 4 the density of pigeons remained the same over the winter at high clover densities but increased at low densities as surplus birds or flocks were forced to use these areas as the total supply of food decreased. While at first apparently vindicating the contention that the pigeons were living close to their food supply it now seems more likely that we were witnessing the first stage of population regulation in relation to the food supply.

One important question remains. Why did not those individuals forced to experience poor feeding conditions leave the flock and feed comfortably nearby? Why even instead of being found at the front of the flock did not these birds follow up in the rear keeping near enough to satisfy their gregarious impulses but far enough away to avoid conflict situations? In fact, it might be thought that the rear of the flock would be the obvious place because rear birds pass over ground already searched by van birds. We have no explanation for the mechanics involved in this ancillary problem and while the general question might be answered on the basis of group-selection the next section explains why this is not really tenable, at least on present knowledge.

(b) *The function of gregarious behaviour*

It is easy to demonstrate that a species behaving as a flock so that competition is introduced at all stages can more effectively exploit the food supply and leave more survivors than a species that feeds in a solitary way and avoids competition until food stocks reach a critical level. Elsewhere a diagram is presented to illustrate this in a simplified way (Murton 1965b), but the basic idea is that if a population of fifty birds has to live on a food supply of 200 items for a limited period and that to survive each bird needs five items, then clearly there is enough food to ensure that forty birds survive. A survival rate approaching this value might be achieved if competition occurred at all times so that some birds were excluded from feeding. Without competition each bird might eat four food items and then the population would have to become extinct. The highest survival rate must be correlated with the highest level of competition that can be achieved. But although a bigger population could survive with gregarious behaviour the advantages would reside only with the surviving animals and another mechanism would be needed to explain why some birds did not break the rules.

Elsewhere (Murton & Isaacson 1962) it was argued that gregarious behaviour would facilitate food finding because only those individuals that had located worthwhile feeding grounds would stay and so could then attract others. The evolution and maintenance of the habit could be explained satisfactorily on this basis without advocating any other function although additional advantages might follow once gregarious behaviour became established. Defence against predators is also often advocated as a function of gregarious behaviour but it seems unlikely to be an important factor in the case of the wood-pigeon. There are no important predators of feeding wood-pigeons in Britain today while the goshawk (*Accipiter gentilis*) and fox (*Vulpes vulpes*) seem the only ones likely to have been important at any time. Goshawks are mainly woodland species and hunt to some extent like the sparrowhawk (*A. nisus*) by dashing round a corner and catching a bird by surprise. It has yet to be shown that gregarious behaviour would reduce the risk from such attack and even if it did it might result in fewer predators—not more pigeons. Thus in general it seems that vertebrate predators are limited by prey density and not prey density by their enemies, a situation that would need to exist to justify the predation defence theories (Errington 1946; Jenkins, Watson & Miller 1964). Hinde (1952) found that flocks of tits tended to disperse at the end of the day when food collection became less imperative but before the birds returned to their roosting holes. A predator could easily adapt to such laxity if the habit really was a predator defence. In the case of the wood-pigeon it would be desirable to discover selective pressures that are currently operative rather than rely on claims that flocking is a relic from days when predation was more important. If predation ceased to be important its selective pressure would immediately be lost and if no other considerations were involved any anti-predator mechanisms would likely be lost at the same time. It seems more reasonable in the wood-pigeon (and perhaps many other species) that gregarious behaviour is directly concerned in some way with feeding or the finding of food, even though anti-predator defences can be found.

The results of this study seem in many ways to support the ideas recently put forward by Wynne-Edwards (1962) that the close adjustment between animal populations and their physical requirements, particularly food, is a manifestation of a self-regulatory process. Wynne-Edwards has argued that population homeostasis has evolved to prevent animals from over-exploiting their resources which implies that natural selection has favoured a mechanism that enables a population to anticipate mortality and make its own

adjustments to numbers or density. The regulation of the animal's reproductive rate in anticipation of possible population replacement requirements is but one aspect of his thesis and is not pertinent to the present discussion, although, of course, winter mortality is a facet of all population loss. Particularly relevant here is his theme that 'unchecked competition for food must be successfully averted, otherwise "over-fishing" would be impossible to escape; this could only result in lasting detriment to the predators and the risk, if they persisted in it, that the prey might be exterminated altogether'. Wynne-Edwards argues that if vast overcrowding occurs when a good food supply exists the animals could over-exploit the resources. Nonetheless this did seem to happen when wood-pigeons were suddenly forced by heavy snow falls to feed on a limited *Brassica* supply in the 1962–63 winter, a situation that could not be anticipated by the population. He further argues that an optimum population density is one that could be supported throughout the period of limited food supplies and to achieve this a limit would need to be set on population-density from the beginning. Exactly how this could be achieved is uncertain because pigeon numbers varied considerably at the beginning of each winter relative to clover stocks because numbers had been adjusted to grain supplies independently of clover availability. The population has ranged between 25 and 174/100 ac in December and there seems no reason why much higher densities could not be attained. There is no evidence that the mechanism of population control would fail providing intensive competition could occur between birds. But regulation would occur if pigeons fed in a solitary way as a point would eventually be reached at which competition could no longer be avoided and single birds like flocks could actively or passively become distributed and their numbers adjusted according to food density. The only difference would be that numbers would fall to a lower level and population fluctuations from the breeding season to the period of winter minima would become more extreme. Again the 1962–63 winter was an example of what does sometimes happen. Even so, there can be no doubt about the advantages of introducing early social competition, and our views on this aspect are in accord with those of Wynne-Edwards. The crucial question, however, is whether the flock behaviour of the wood-pigeon (and for that matter other species) has evolved primarily as a homeostatic mechanism—which Wynne-Edwards would claim to be the case—or whether the mechanism of population control operates through a social behaviour that has evolved as a result of other selective pressures. The environment must determine population size, otherwise there would be no consistent variation in bird density in different areas or seasons; but in the first instance the adjustment would involve an intrinsic and active adaptation by the animal, in the second case a passive response to extrinsic environmental pressure.

Wynne-Edwards (1962) maintains that natural selection may favour the group at the expense of the individual. In a very restricted sense this may be true because the gene pool of the Mendelian population sets limits on the genetical diversity of the individual genotypes which must be limited by the variation available from the gene pool. If this in turn contains many factors for social behaviour this might modify the evolutionary process. Haldane (1934) showed many years ago that natural selection can only operate on those individual genotypes which have been entrusted with temporarily carrying the variability available from the gene pool. Recently Wynne-Edwards (1963) has maintained that genetical evidence for group selection does exist and Smith (1964) has given the mathematical requirements for group or kin selection. However, Smith shows that the conditions that have to be satisfied are so special and severe that it seems extremely unlikely that they could operate under field conditions for most, if not all, bird species.

Because at present there appears to be no satisfactory genetical basis for group selection of the sort discussed above, social behaviour ought first to be considered in terms of its advantages or disadvantages for the individual. Gregarious behaviour in the wood-pigeon might evolve because those individuals reacting positively to other feeding birds would have much better chances of locating suitable food sources and as a result have higher survival chances. Social behaviour would then facilitate a hierarchy system which could ensure earlier competition between individuals and the exclusion of surplus birds or flocks to other feeding grounds. This could also lead to a higher survival rate relative to food as discussed above and the process could reinforce social behaviour, but it need not be the cause. The mechanism of population control through social behaviour could, therefore, be fortuitous and be explainable on the grounds of individual selection. At present this view is preferred in the absence of a satisfactory genetical theory.

### ACKNOWLEDGMENTS

We are grateful to Dr J. M. Cullen and Dr D. Lack for critical comment on the ethological and ecological views expressed in this paper. It is a pleasure to thank Dr I. Thomas and Mr H. V. Thompson for carefully reading this paper and for offering many suggestions for improving the text. Professor Wynne-Edwards has given much editorial guidance while we have also benefitted from discussions with him and members of his Department and also from the referee's comments. Mr A. G. Jenson kindly prepared the figures from our original rough drawings.

### SUMMARY

1. This paper describes the relationships between a wood-pigeon population and its clover food supply over six winters (November to March) in a study area of 2647 ac of arable farmland in Cambridgeshire.

2. Wood-pigeons were counted during standard census walks; some shot birds and others caught with stupefying baits were weighed, aged and examined; feeding birds were observed for long periods and their behaviour recorded. The clover availability was measured by counting the number of leaves in sample foot squares throughout the area. The number of leaves eaten was recorded under some conditions and in addition protective enclosures were erected to prevent the birds from feeding on control plants.

3. Wood-pigeons regularly ate over 50% of the clover stocks in mid-winter but damaged crops recovered in early spring when clover growth was rapid and usually there was no difference between control plots (where no clover was eaten) and damaged areas by May. The clover was able to recover in two months when 89% was artificially destroyed by cutting to simulate very intensive damage.

4. In 1961-62 the percentage decrease in clover density on different fields between November and late January/early February was unrelated to original density when stocks had been above about 150 leaves/ft<sup>2</sup>, but proportionately more survived when initial densities were below this value. The reasons are given for attributing this to an absence of pigeons feeding at low clover densities; differential growth, weather damage or farm stock grazing could not account for the result. In 1962-63, when pigeons were unable to feed owing to a persistent snow blanket, clover changes caused by growth and weathering were density-independent for all clover densities. More leaves could be identified as eaten by pigeons at high clover densities, but not proportionately more.

5. Wood-pigeons were sometimes noticeably distributed according to clover density. Sometimes they clearly avoided fields with little clover (fields with less than 100 leaves/ft<sup>2</sup>) and this was particularly so in January, but later in the season in February flocks were found on areas of poor clover stock. There was some evidence that more mortality occurred in the flocks inhabiting poor fields (including emigration as mortality) because in one year (1964) bird density remained stable at high but declined at low clover densities. Some other observations showed that the mean weight of pigeons in those flocks feeding at very low clover densities was significantly lower than that of birds in flocks feeding on good fields. In 1965 pigeon density declined on both good and bad fields, though it seems likely that this was because the original total population was much higher than in 1964.

6. Wood-pigeons fed gregariously and less than 1% fed in groups smaller than five individuals. The gregarious habit is shown to be very ingrained. The feeding rate varied throughout the flock and birds in the middle and rear obtained significantly more food items per unit time than those in the front. Some preliminary evidence is given to show that pigeons have a stable flock structure, so that on average each bird maintains the same position relative to others. It is not known whether a true social hierarchy exists, with the birds able to recognize each other as individuals. Front birds obtained significantly less food than the others over long periods.

7. The food collection rate (number of pecks per minute) did not seem to vary with clover density throughout a wide range of values, partly because the birds increased their searching rate (number of paces per minute) to compensate. However, at densities below 100 leaves/ft<sup>2</sup> the pecking rate did decline with clover density. When the feeding rate fell below an optimum level for satisfactory food intake the front birds were affected first. Some birds were seen to be collecting insufficient food. With a constant food density the rate of intake decreased with an increase in searching rate. Because the searching rate declined in the late afternoon, to enable the intake rate to increase, it seems likely that the birds were more selective in what they consumed in the first part of the day.

8. Most of the birds in the population remained in good condition, judged by their body weights, irrespective of the total food supply, but the proportion in very low weight classes varied, not with the food supply, but in relation to the mortality rate that was governed by the food supply and population size. Hence, proportionately more starving birds were seen when the winter mortality rate was high. Because differential mortality through starvation or enforced emigration occurred the total population size was positively correlated with clover availability in 5 years of study. In one year continuous and steady competition in the flock was disturbed because heavy and persistent snowfalls forced a high population into sudden and intensive conflict for a very limited *Brassica* food alternative. Instead of a few starving birds being found nearly the whole population suffered a reduction in body weight at the same time. Juveniles suffered more severely than adults from food shortages but there were no differences between the sexes.

9. The relationships between food collection rates and searching area are discussed in connection with flock behaviour and a mechanism for competition is demonstrated. Pigeons leaving the feeding flocks departed mainly from the front. Similarly, birds arriving at the flock settled in the front or rear and very rarely in the centre. It is suggested that a kind of 'social hierarchy' was responsible for this behaviour and that submissive individuals avoided intra-specific conflict situations. It is suggested that if flock size is too high relative to food availability some birds have feeding rates below an optimum threshold and under these conditions they leave the flock to forage elsewhere. In practice

they would try to feed with other flocks. In this way the flocks could become adjusted to the food supply and some flocks would be forced to use areas of poor clover availability, whence mortality could occur but normally only a few individuals would die at a time.

10. It is contended that social factors can be involved in ensuring competition and the highest survival rate relative to food supplies. However, this mechanism of population control could have become adapted to a social behaviour that evolved for other reasons. The possibility that group-selection was involved (Wynne-Edwards 1962) and prevented birds from 'free-lancing' is discarded; partly because an adequate genetical basis for the theory is lacking, and partly because it seems possible that the advantages of gregarious behaviour for population control are a secondary benefit of a behaviour maintained through other survival advantages.

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(Received 22 July 1965)

Appendix 1. *Percentage composition of clover leaf samples collected from five fields at Carlton in 1961 (Based on absolute dry matter)*

	Field				
	E	45	105	211	FL
Crude protein	30.3	25.0	27.4	29.9	33.5
Oil (ether extract)	3.0	2.8	3.9	2.8	3.0
Crude fibre	16.6	12.1	13.0	9.3	12.7
Nitrogen-free extractives	30.9	32.5	30.9	43.8	32.4
Total ash	17.2	27.6	24.8	14.2	22.4
Siliceous matter	9.3	19.8	17.6	5.7	15.1
Silica-free ash	7.9	7.8	7.2	8.5	7.3
CaO	1.44	1.24	1.45	1.26	1.30
P <sub>2</sub> O <sub>5</sub>	0.73	0.69	0.50	1.12	0.72
K <sub>2</sub> O	1.93	1.90	1.20	2.58	1.70
NaCl	0.06	0.16	0.20	0.44	0.16
True protein	28.0	22.1	25.2	24.6	25.8



Appendix 2. *Distribution of wood-pigeons at Carlton in relation to clover density in 1964*

Field	Acreage	Clover per square foot in January		No. pigeons feeding on 7 Jan.	Field	Clover per square foot in February		No. pigeons feeding on 5 Feb.		No. pigeons feeding on 19 Feb.		No. pigeons feeding on 20 Feb.		Average pigeon density 1-4/ac on 5-6 February	Average pigeon density 1-5/ac on 19-20 February
		(1934)	(1964)			(1964)	(1964)	(1964)	(1964)	(1964)	(1964)				
5*	22	107	91	107	4*	24	233	24	6	2	19	3	158	1.4/ac	1.5/ac
56*	32	24	22	176	6B	29	218	11	11	86	48	68	74	1.4/ac	1.5/ac
46*	12	219	92	219	46*	31	(198)	61	113	51	74	78	6	1.4/ac	1.5/ac
11A	36	7	14	7	56*	97	(182)	131	54	170	36				
11B	29	250	53	250	11A	135	145	135	6						
66B	22				11B	135	152								
297	1				11C	135	135								
4	40				4A	130	130								
24A	24				4B	107	107								
6	18				300	96	96								
211	36	10	1	10	247	93	93								
221	60				6	90	90	46	21	32	25	26			
300	6				38	84	84	6	74	11	20	20			
4B	19				221	65	65	6	45	54	11	11			
11D	28	68	369	68	215	62	62	91	87	14	20	20			
218	28				244	52	52	158	11	16	96	96			
13A	27				13A	49	49	7	11	12	72	72			
9A	13	7	56	7	110	48	48	7	100	240	42	42			
69	11				223	45	45	2	168	7	1	1			
4C	23				4C	45	45		56	18					
14A	9	5		5	218	41	41								
109	2				6A	41	41								
222	6				20	40	40								
19	19				11D	37	37								
215	16	76	80	76	69	33	33								
38	23				66	30	30								
20	21				205	24	24								
111	6	119	51	119	239	24	24								
239	14				220	21	21								
107	14				107	19	19								
205	25				109	18	18								
37	18				14A	15	15								
223	12				11C	11	11								
110	10				37	3	3								
220	2				222	0	0								
11C	6				111	0	0								
9	6				9	0	0								
217	4				217	0	0								
251	8				251	0	0								
253	20				253	0	0								
Total feeding		1068	855	855	Total feeding	1196	968	832	713						

\* These were stubbles and the clover count was multiplied by 3.8.

Appendix 3. Distribution of wood-pigeons at Carlton in relation to clover density in 1965

Field	Acreage	13 Jan.		14 Jan.		10 Feb.		11 Feb.		10 Mar.		11 Mar.	
		No. pigeons feeding	Clover per square foot in January	No. pigeons feeding	Clover per square foot in January	No. pigeons feeding	Clover per square foot in February	No. pigeons feeding	Clover per square foot in February	No. pigeons feeding	Clover per square foot in March	No. pigeons feeding	Clover per square foot in March
49*	26	298	(954)	209	207	35	(825)	54	99	49*	(506)	40	49*
50A*	13	10	(570)	55	181	59	374	25	72	4	475	60	4
106*	12	4	(422)	335	171	40	300	2	4C	4A	381	32	4A
4	40	10	351	140	181	450	274	3	66	44*	(342)	190	1
4A	8	4	320	58	161	261	300	2	9A	11*	(232)	9	47
44*	9	23	(293)	25	153	40	274	3	9A	50A*	(237)	9	14
48A*	4	57	(224)	13	133	142	(220)	11	4C	11*	(217)	80	18
66A	36	209	224	500	181	72	164	11	106*	50A*	(208)	17	63
211	36	209	207	2	181	14	(152)	5	221	106*	(194)	10	45
6B	22	209	183	2	171	14	140	5	221	6B	198	9	18
221	60	209	181	2	171	14	117	5	48A*	8*	(148)	4	8*
247	3	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
9A	13	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
6	18	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
229*	13	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
244	24	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
8*	37	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
107	25	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
4C	23	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
11*	42	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
6A	19	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
66	9	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
300	6	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
11A	36	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
222	11	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
66	11	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
11D	28	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
215	16	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
11B	29	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
218	28	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
14A	9	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
217	4	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
100	2	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
105*	18	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
13A	27	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
205	2	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
223	12	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
223	12	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
24B	10	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
110	10	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
0	6	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
3B	8	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
11C	6	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
111	6	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
230	14	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
237	18	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
253	20	209	161	2	171	14	117	5	48A*	8*	(133)	4	18
Total feeding		1726	1545	1807	1596	950	744						

\* These were stubbles and the clover count was multiplied by 3.8.