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Using Leslie matrices to determine wild rabbit population growth and the potential for control

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Summary

1. Data on fecundity and mortality obtained from wild rabbit *Oryctolagus cuniculus* populations in England were used in Leslie Matrix population projections to examine rate of population growth and the effect of time of control on population growth.

2. The population growth rate was shown to be slightly greater than unity in an average year.

3. Control policies which remove more adults than juveniles are best performed at the end of December and policies which remove more juveniles than adults are best performed in mid-June.

4. The limitations of the model used are discussed, as are limitations in the data. It was concluded that more information was required on natural mortality rates, especially fot the first few weeks of life.

Key-words: Leslie matrix, models, *Oryctolagus cuniculus*, population control, rabbit.

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Introduction

In 1953 47% of agricultural holdings in England were heavily infested with rabbits *Oryctolagus cuniculus* (L.) but within 3 years over 99% of the rabbit population had been killed because of the introduction of myxomatosis in the autumn of that year (Lloyd 1970). In the years following the introduction of myxomatosis, the relationship between the virus and the rabbit has changed, with an initial reduction in the virulence of the virus and an increase in the resistance of the rabbit. Reviews of this changing relationship are given by Ross (1982) and Ross & Sanders (1987). Similarly, changes have occurred in Australia (Marshall & Fenner 1958, 1960) and France (Joubert, Leftheriotis & Mouchet 1972). Despite this changing relationship, it appears that myxomatosis is still an important factor in the regulation of rabbit numbers (Ross & Tittensor 1986; Ross *et al*. 1989) and that predator pressure may also be limiting population growth (Trout & Tittensor 1989).

Although locally rabbit numbers are very variable, it is clear that nationally rabbit numbers are slowly increasing despite current levels of hunting and control (Lloyd 1981; Tittensor 1981; Trout, Tapper & Harradine 1986). It would be advantageous to be able to predict the population growth rate, how variable this rate is, and what level of rabbit control

is necessary to prevent local populations from causing economic damage to crops and horticulture. Computer modelling has been used to simulate myxomatosis spread (Dwyer, Levin & Buttel 1990; Seymour 1992) and rabbit management as a harvestable crop (Walsingham, Edelsten & Brockington 1977); however, modelling the management of wild rabbits as a pest has received little attention in comparison to the number of field studies.

It is likely that the effect of any control policy, in terms of percentage kill and potential for recovery, will be dependent on the time of year during which it is implemented, and determining how rabbit control interacts with the annual population cycle would help increase the effect of any such policy. This paper details an initial attempt to derive these factors using Leslie Matrix population projection in a similar approach to that used for New Zealand rabbit numbers by Darwin & Williams (1964). A basic deterministic, density-independent approach was used to simplify the analysis on this first approach to modelling British rabbit population growth, and the limits of this approach, along with the identification of the important variables of the rabbit population are raised in the discussion. As more data become available it should be possible to produce more complex, but realistic models of rabbit control.

The model

The use of matrix algebra in population biology has received considerable attention since Leslie (1945, 1948) proposed it to project population densities. In its simplest form a female population is divided into m age groups, with the number in each age group at time t defined by the vector

$$\mathbf{N}_t = (n_{0t}, n_{1t}, \ldots, n_{mt})^{\mathrm{T}},$$

and the total population size at time t by

$$N_t = \sum_{i=0}^{m} n_{it} \qquad \text{eqn 1}$$

where n_{it} is the number of females in the age group i to $i + 1$ at time t, and $()^{\mathrm{T}}$ is the transpose of the matrix. The change in population structure from time t to time $t + 1$ is then represented by the equation

$$\mathbf{N}_{t+1} = \mathbf{L}\mathbf{N}_t,$$

where $\mathbf{L}$ is a Leslie Matrix. The matrix $\mathbf{L}$ is a square matrix of order m, where the first row is the expected number of female offspring, f_i ($f_i > 0$), produced by an individual of age i, and the first subdiagonal contains the probability of survival, p_i ($0 < p_i < 1$), from one age group to the next. This matrix is therefore of the form:

$$\mathbf{L} = \begin{bmatrix} f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_1 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & p_{m-1} & p_m \end{bmatrix} \qquad \text{eqn 2}$$

Since the standard Leslie Matrix assumes that animals in the final age-class die with a probability of 1·00 during the time interval t to $t + 1$ no animal can survive to an age greater than m. To permit the extension of the duration of life of an individual the (m, m) element of matrix $\mathbf{L}_j$ can be set to a proportion p_m if it can be assumed that mortality and fecundity of this class remain constant for the remainder of the life of that individual. This parameter will be referred to as the final age survivorship value.

The dominant eigenvalue, λ, of the matrix $\mathbf{L}$ defines the rate of growth of the population. When λ equals 1·00 the population size is stable. This value is equal to the antilog of the per capita rate of increase, r;

$$r = \ln \lambda. \qquad \text{eqn 3}$$

The eigenvector associated with the dominant eigenvalue gives the age-stable population structure. Therefore, successive age-stable populations are defined by the non-trivial solution

$$\mathbf{N}_{t+1} = \lambda \mathbf{N}_t; \; n_{it} > 0, \; N_t > 0, \; t > 0, \; 0 < i \leq m, \qquad \text{eqn 4}$$

and the rate of growth of the population is

$$(\mathbf{N}_{t+1} - \mathbf{N}_t)/\mathbf{N}_t,$$

which reduces to $\lambda - 1$ given equation 4. Thus, when $\lambda > 1$ the population size is growing, when $\lambda = 1$ the population size is stable and when $0 < \lambda < 1$ population size is decreasing.

In this basic form the model is both deterministic and density-independent. Boyce (1977) has shown that if a stochastic element is introduced to the matrix $\mathbf{L}$, the expected population size at time t (equation 1) decreases with an increase in the standard deviation σ of parameters, p_i and f_i. Thus, results from the deterministic matrix should be assumed to be maximal values for when $\sigma = 0$.

Levels of density dependence can also be built in to the matrix $\mathbf{L}$ such that the survival and/or fecundity parameters can be related to $\mathbf{N}_t$ to produce a matrix $\mathbf{L}_{n(t)}$.

In the following analysis the simple matrix form is assumed with no density-dependent survival or fecundity included. This approach has been chosen to simplify the analysis of the underlying population parameters since it is necessary to examine each variable for its sensitivity on the overall model. The issues of density dependence and long-term population forecasting will not be considered in this paper as their inclusion would be meaningless without equally detailed information on man-induced rabbit population control.

Suppose that in equation 2 the f_i and/or p_i are themselves dependent on time of year and follow an annual cycle, as well as being dependent upon age. For such a case each year y can be divided into s equal units of time of duration equal to t to $t + 1$. Then in the jth unit of the year a female of age i will give birth to f_{ij} female young, and it will survive to become age $i + 1$ at time $t + 1$ with a probability of p_{ij}. These parameters then form the matrix $\mathbf{L}_j$. After a time of 1 year (s units of time) the new population will be represented by

$$\mathbf{N}_{y+1} = \mathbf{L}_s \mathbf{L}_{s-1} \ldots \mathbf{L}_1 \mathbf{N}_y. \qquad \text{eqn 5}$$

Suppose that at some time during the year a control policy is implemented which removes a proportion x of age group i denoted by x_i. A matrix $\mathbf{H}$ can be constructed where all elements are zero except for the main diagonal, which contains the values of $(1 - x_i)$. If this control is implemented between the jth and $(j + 1)$th units then equation 5 becomes

$$\mathbf{N}_{y+1} = \mathbf{L}_s \mathbf{L}_{s-1} \ldots \mathbf{L}_j \mathbf{H} \mathbf{L}_{j+1} \ldots \mathbf{L}_1 \mathbf{N}_y, \qquad \text{eqn 6}$$

and λ, the dominant eigenvalue of the matrix

$$\mathbf{L}_H = \mathbf{L}_s \mathbf{L}_{s-1} \ldots \mathbf{L}_j \mathbf{H} \mathbf{L}_{j+1} \ldots \mathbf{L}_1$$

defines the rate of growth of the population from year y to $y + 1$ including any effects of the control policy. It is assumed here that rabbits are divided into two age categories (young and old, both containing one or more age groups) and a particular

strategy of control produces a differential survival probability in each category.

The value of λ can be calculated directly with specific software packages or estimated iteratively by successive premultiplication of a vector N_0 until each element N_{t+1} is in the same ratio as the corresponding element of N_t. This latter method was employed for convenience and λ has been estimated to two decimal places.

Data base

The rabbit population parameters used in this analysis were derived from two sources. Data on rabbit fecundity originate from post-mortem examinations of 1370 does collected from 15 sites in England between 1981 and 1983.

The sample of 1370 does were placed into one of 13 4-week periods of the year depending upon the expected time of birth of any embryos present, and aged by the degree of lumbar epiphyseal fusion into four categories (0 fused epiphyses, 1−6 fused epiphyses, 7−13, and 14 fused epiphyses; Trout & Lelliot 1992). A fifth age category of females too young to breed was included in the model. The five categories correspond approximately to animals aged up to 19 weeks old, 20−43 weeks old, 44−71 weeks old, 72−103 weeks old, and older.

The number of well developed implanted embryos (greater than 20 days old) present per pregnant female in each 4-week period was recorded, and a smooth interpolation made by eye. This number was then reduced by 50% to represent the number of female offspring born per doe in each age-class. The proportion of females with implanted embryos in any period was increased by an additional 20% to account for females in the first 6 days of pregnancy, prior to implantation, which would not have been detected during the post-mortem. Table 1 presents

the final productivity data by time of year and age of female.

The mortality data were derived from a study on the free-living rabbit population of Aston Rowant National Nature Reserve between 1976 and 1983. The site and population are described by Cowan (1987a,b). Myxomatosis was present in the population during most years, but only three epizootics coincided with marked reductions in the minimum population estimates. This resulted in a large variation in survival between years. For the mortality rates for females from 4 to 52 weeks of age, the data from Table 1 of Cowan (1987a) were used to derive a mean estimate of the survival probability of 0·08. For females from 1 to 2 years old an annual survival figure of 0·44 was used, and for older females a value was interpolated from the graph (Cowan 1987a, p. 64) to give an annual survival of between 0·40 and 0·69.

Other studies of rabbit populations have found a low survival rate in the first few weeks post-emergence (Richardson & Wood 1982; Wheeler & King 1985), but survival in the first few weeks of life, prior to emergence, has not been directly measured in a natural population. Wood (1980) indirectly measured this survival rate at 0·51, 0·12 and 0·19 in Australian rabbits under arid conditions. These figures must be considered as absolute minimum values for British rabbits. In this analysis survival of rabbits from birth to 4 weeks of age was conservatively assumed to be 0·90 and the sensitivity of this parameter was examined.

To permit an analysis of 'good' and 'bad' years for juvenile survival, the probability of survival was adjusted to 0·11 for 'good' years and 0·02 for 'bad' years. These figures fall within the annual variation of survival for the Aston Rowant rabbits (Cowan 1987a,b) derived from sightings and capture−recapture on the site. Survival rates for

Table 1. Female productivity in each 4-week period of the year. For each period the number of female offspring produced per female of each age category is given

| Period | Time of year | Age of female (weeks) | | | | |
		0−19	20−43	44−71	72−103	104+
1	1 Jan. −28 Jan.	0·00	0·00	0·37	0·59	0·42
2	29 Jan. −25 Feb.	0·00	0·83	1·24	1·35	1·00
3	26 Feb. −25 Mar.	0·00	1·30	1·74	1·92	1·42
4	26 Mar.−22 Apr.	0·00	1·40	2·00	2·30	1·70
5	23 Apr.−20 May	0·00	1·12	1·98	1·50	1·80
6	21 May −17 Jun.	0·00	0·63	1·13	0·92	0·92
7	18 Jun. −15 Jul.	0·00	0·30	0·57	0·58	0·57
8	16 Jul. −12 Aug.	0·00	0·12	0·35	0·38	0·33
9	13 Aug.−9 Sep.	0·00	0·00	0·18	0·25	0·18
10	10 Sep. −7 Oct.	0·00	0·00	0·00	0·00	0·00
11	8 Oct. −4 Nov.	0·00	0·00	0·06	0·00	0·00
12	5 Nov.−2 Dec.	0·00	0·00	0·07	0·03	0·03
13	3 Dec.−31 Dec.	0·00	0·00	0·08	0·14	0·20

each 4-week period were adjusted proportionately to achieve the above annual survival probabilities. No assumption was made on the cause or causes of high or low juvenile survival, and the definition of a 'good' or 'bad' year was made entirely on the survival probability. Survival during these years may be related to environmental factors such as weather, or density-dependent factors such as disease.

Successful female natal dispersal between warrens in the above population was measured at 32·9% (Cowan 1991). No data on emigration from the population were collected, therefore, taking into account the geographical distribution of warrens, a conservative adjustment of a 10·0% emigration from this population was made, and the mortality rates adjusted to compensate. This permitted the model population to be considered in isolation, with no immigration or emigration. The final survival probabilities for all three types of years are presented in Table 2. No attempt has been made to adjust survival probabilities of each age group by the time of year (since exact figures are not available for mortality rates in some age groups at certain times of year), so in this preliminary model mortality is assumed to be constant throughout the year.

Analysis

THE MODEL

By using the above parameters, and assuming that no females survive beyond 2 years of age ($p_m = 0$), the calculation of the dominant eigenvalue produced a figure of 1·24 for λ. With the adjustments in juvenile mortality a figure of 1·61 was found for a good year and 0·48 for a bad year. Various levels of final age survivorship were examined to account for survival beyond a 2-year limit. For animals in the final age-class 4-weekly survivorship p_m was related to annual survivorship A by

$$A = p_m^{13}$$

if p_m is constant throughout the year. Figure 1 shows the rate of population growth for all three types of years against the annual survivorship value. The increase in the rate of growth with an increase in annual survivorship was greatest for years with low juvenile survivorship, and was similar for both average and good years of juvenile survivorship.
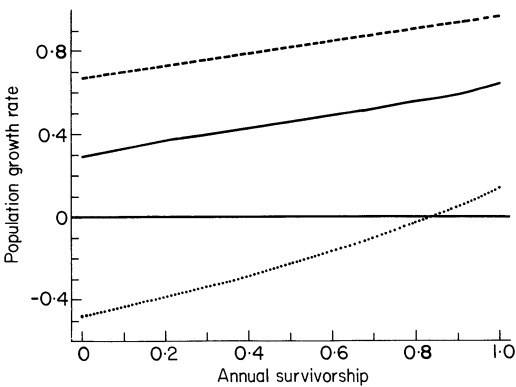

Fig. 1. Variation in the population growth rate $\lambda - 1$ with increasing annual survivorship of females greater than 2 years old (p_m). The solid line is for a year of average juvenile survivorship, the dotted line a bad year for juvenile survivorship and the dashed line a year of good survivorship.

This graph shows the contribution of the older animals to the population growth in years of varying juvenile survival. For the remaining experiment a final age 4-week survivorship value of 0·90 was chosen. Overall, the inclusion of a value for p_m resulted in λ becoming 1·38, 1·75 and 0·64 during a normal, good and bad year for juvenile survival.

EFFECT OF CONTROL POLICY

To examine the rate of population growth under various control policies, two age categories of rabbits were defined which undergo differential survival. Two categories were chosen for the sake of simplicity, but it is more likely that within each category each age group i will have a slightly different survival rate from the others. The two age categories chosen are 'young' and 'old', with the maximum age of young rabbits increasing in 4-week intervals from 4 weeks to 32 weeks. A survival rate of 0·95 for young rabbits and 0·05 for old rabbits was used to accentuate any differences present between the two categories. The effect of this control policy during the year is shown in Fig. 2 for a year of otherwise normal juvenile survival. The x-axis of Figs 2–5 begins on the third 4-week period (25 March) so that all maxima and minima are correctly shown. In Fig. 2 the most fundamental change is with increasing maximal age of the young, where there is an increase in the growth rate regardless of the time

Table 2. Probabilities of a female rabbit surviving from the beginning of one age category to the beginning of the next 4-week period, for a year with 'average', 'good' and 'bad' juvenile survival

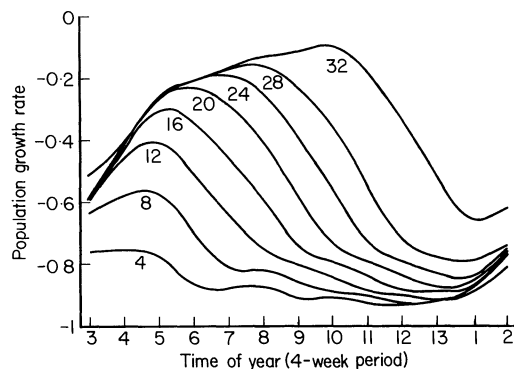| Type of year	Age (weeks) 0	4	8	12	16	20	24	28	32	36	40	44	48	52	··	96
Normal	0·90	0·48	0·72	0·80	0·81	0·81	0·83	0·82	0·90	0·93	0·90	0·99	0·99	0·94	··	0·94
'Good'	0·90	0·52	0·75	0·83	0·83	0·83	0·85	0·84	0·92	0·95	0·92	0·99	0·99	0·94	··	0·94
'Bad'	0·90	0·40	0·64	0·72	0·73	0·73	0·75	0·74	0·82	0·85	0·82	0·91	0·91	0·94	··	0·94

Fig. 2. Variation in the population growth rate $\lambda - 1$ with time of year of a control policy from which 0·95 young and 0·05 old animals survive. The lines represent the maximum age of a young rabbit, from 4 weeks to 32 weeks of age. The categories of young and old refer only to the variation in survival rates from a control policy.

Fig. 3. Annual rate of increase of the population, as measured by $\lambda - 1$, with varying time of control, under seven different control policies (see text). The data assumed that the year is an average one for juvenile survival.

of the control. This is merely a result of the increased proportion of the entire population which survives the control policy. However, as the maximum age of the young rabbits increased, the variation of the rate of growth with timing of the control increased. Over-all, λ is greatest between periods 5 and 10 (late April—early September) and least between periods 12 and 1 (November—January).

In the following analysis, a young animal is defined as up to 20 weeks of age and the whole population underwent rabbit control to examine the effect on population growth of control policies with different success rates. In addition, different methods of rabbit control will produce differential mortality among old and young rabbits. To simulate this effect seven different levels of control were used, with a survival for young and old animals as follows:

H_1, 0·95, 0·05; $\quad$ H_2, 0·95, 0·25; $\quad$ H_3, 0·95, 0·50;
H_4, 0·95, 0·95;
H_5, 0·50, 0·95; $\quad$ H_6, 0·25, 0·95; $\quad$ H_7, 0·05, 0·95.

No attempt will be made at this stage to match up any of the above levels of control with specific methods of rabbit control. In all cases the last age survivorship value p_m was set conservatively at 0·90 (from Cowan 1987a), and control was performed once during the year. The result of these policies on the growth rate is shown in Fig. 3. Figure 4 shows the same policies executed during a year of good juvenile survival and Fig. 5 during a bad year for juvenile survival. All three figures show a similar pattern with the timing of the control policy. A control policy which kills a greater proportion of the old animals has the greatest effect, in terms of reducing λ, when performed during the winter months (periods 10–2; mid September—late February). If the control policy kills a greater proportion of young animals, λ is lowest when such a policy is performed between late March to mid August (periods 4–8). This suggests that a control policy from which 95% of the young
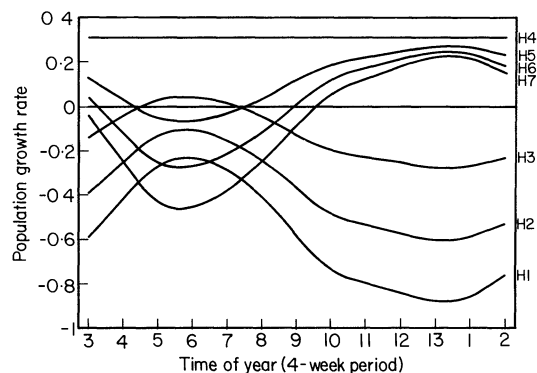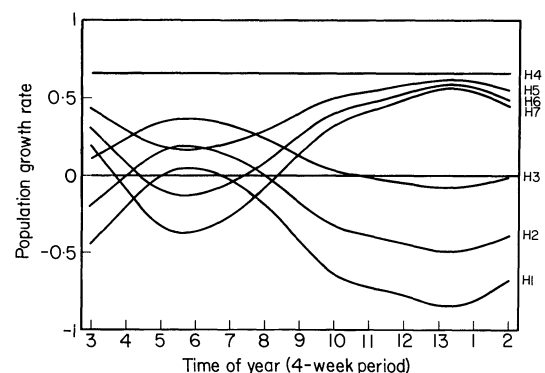

Fig. 4. Annual rate of increase of the population, as measured by $\lambda - 1$, with varying time of control, under seven different control policies (see text). The data assumed that the year is above average for juvenile survival.
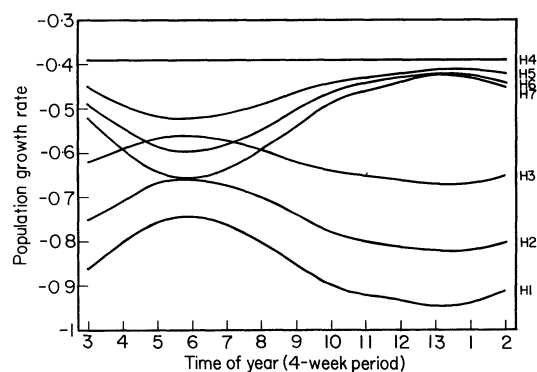

Fig. 5. Annual rate of increase of the population, as measured by $\lambda - 1$, with varying time of control, under seven different control policies (see text). The data assumed that the year is below average for juvenile survival.

rabbits survive and 25% (H_2) of the old survive would reduce the population to 0·39 of its original value in 1 year if performed at the end of December, but to only 0·90 if performed in mid June. If this policy were performed in December this model shows that the population would take 3 years of uncontrolled growth to return to its original value,

while if performed in June, the population in the following year would be 1·2 times its original size. Note that this model takes no account of any density-dependent factors which could influence these figures. If such a control policy were only performed during years when the population is obviously growing fast then λ is only reduced to 0·50, taking just over 2 years to recover, while if performed during a poor year λ is reduced to 0·18 and the simulated population would take nearly 6 years to recover. The above assumes that recovery occurs during average years.

The age-stable distribution, at the end of May, is shown in Fig. 6 for three populations: (a) an uncontrolled population (or policy H₄); (b) a population with H₁ applied at the optimum time, at the end of December; (c) a population with H₆ applied at the end of December.

It can be seen that when the population proportion resulting from (b) is lower than the uncontrolled population (a), then the opposite policy (c) has a higher proportion. Throughout the age range the deviation from the proportions in the uncontrolled population (a) are greater for (b) than the deviations resulting from policy (c). This appears to show that an optimum control policy which kills a greater proportion of old rabbits than young disturbs the age-stable population distribution by a greater amount than the reverse policy.
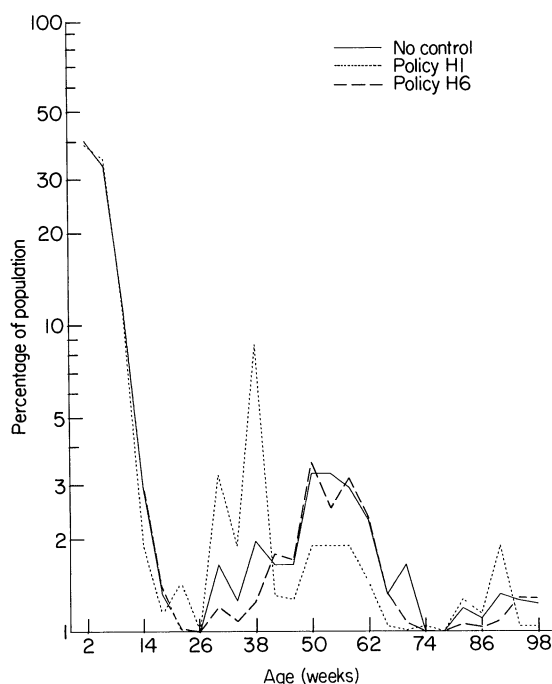

Fig. 6. Age distribution at the end of May, of an age-stable population with no rabbit control, and with control policies H₁ and H₆ implemented at the end of December.

SENSITIVITY TESTING

To examine the sensitivity of the model to errors in the estimated population parameters it was decided to adjust each of the calculated variables by a factor of 10%. These parameters were: survival of each 4-week age-group; fecundity of females aged 20–40 weeks; 44–68 weeks; 72–100 weeks; 104+ weeks. In addition, the adjustment of mortality to account for population dispersal (set at 10% in the above analysis) was either excluded or set to 33%. Sensitivity analysis was only performed on the data for an average year of juvenile mortality. Adjustment to juvenile survival (individuals prior to the age of reproduction) of 10% resulted in an adjustment to λ of 8·0%. Adjustments to the survival of reproducing individuals of 10% resulted in a maximum change in λ of 7·2%. An adjustment in the fecundity of individuals resulted in much smaller changes in λ. A maximum change in λ of 3·6% when females from 44 to 68 weeks of age were adjusted by 10% was produced, all other changes resulted in a change in λ of 1·4% or less. This shows a robustness of the model to errors in measures of fecundity since the age categories for fecundity included up to eight 4-week periods.

The removal of the assumption of dispersal resulting in emigration affecting the measured mortality rates by 10% (which results in unadjusted survival rates) reduces λ to 1·14, a reduction of 17·4%. If it is assumed that the rate of emigration is 33% and the survival rates are proportionately adjusted then λ is increased to 1·72, an increase of 24·6%. This must be a maximum figure since it assumes that all dispersal results in emigration. Although these changes have a significant effect on λ for this model population, it will have no effect on the relative level of λ either between 'good', 'bad' and average years, or on timing of the control policy. Thus, while the exact level of λ should be regarded with caution, inferences from a comparison between populations or on time of year should be unaffected by such variation.

Discussion

Rabbit population parameters derived from 16 locations in England have been used in Leslie Matrix population projections. These projections have included varying levels of rabbit control instigated at different times of the year. Sensitivity analysis has shown the model to be very robust to deviations in fecundity and quite robust to deviations in mortality. The age groups which are most sensitive to deviation are the youngest groups prior to the commencement of breeding. However, this model is susceptible to the assumption that dispersal which results in emigration from the population may have adjusted the measured mortality figures. Further analysis with

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this form of population projection will therefore require a more detailed analysis of emigration from the population used to determine mortality levels. However, this will have no effect on the relative results due to the timing of rabbit control or on the relationship between 'good', 'bad' and average years.

By defining 'good', 'bad' and average years as being within the variation in juvenile survival rates found in the Aston Rowant rabbit population comparisons may be drawn between them. In an average year the annual growth rate of the population, $\lambda - 1$, is slightly greater than zero, while in a 'good' year it is above 0·50. During a 'bad' year the annual growth rate is negative, but is more dependent upon the level of survivorship among the older animals than the other two years. This latter result is to be expected since with a higher juvenile mortality a greater proportion of the young born in the following year will be produced by the older animals. It is interesting however, that increased juvenile survival does not appear to have the opposite effect (Fig. 1).

The year was divided into 13 4-week periods, defined in Table 1, and a control policy from which different proportions of young and old rabbits survived was implemented. Any policy which kills a greater proportion of the old rabbits than the young rabbits is best applied during December and January, regardless of the size of the difference in these rates. A policy which kills more young than old is best applied in mid June soon after the peak birth season, and after the young have been exposed to the highest level of natural mortality (aged 4−8 weeks).

The optimum timing of control is independent of the level of natural mortality to which the juveniles are exposed, but the recovery period is longer if the control is performed during a year of low juvenile survival. If predator pressure is additive rather than compensatory, as suggested by Trout & Tittensor (1989), then the recovery period will be even longer than that estimated from this model if control is implemented during a year of low juvenile rabbit survival.

There are important assumptions and limitations associated with the model as described. First, it is deterministic, so the level of variation around any particular value of λ is unknown. Secondly, it is also density-independent, so there is no compensatory reduction in mortality, or increase in fecundity when the population is culled. This limitation will have less effect on control policies implemented just before the breeding season than on policies implemented in late summer. A compensatory reduction in natural mortality has 8 months to have an effect with a policy which kill a greater proportion of young rabbits (policies H_5, H_6 and H_7), but only 2 months on policies which kill a greater proportion of old rabbits (H_1, H_2 and H_3) if these policies are performed at the optimum time to reduce λ. It is likely, therefore, that the shape of the curves defined

by H_5, H_6 and H_7 may be changed by such compensation, resulting in a reduced effect of control.

Thirdly, it was also necessary to make an assumption on the level of juvenile mortality from birth to 4 weeks of age due to the paucity of data covering this period. This period of time is mostly spent underground and is prior to the possibility of capture in traps, the usual means of sampling a population. Indeed, many methods designed to measure this parameter would be invasive and liable to increase the rate of mortality. The sensitivity analysis shows that mortality in this period of life has one of the greatest effects on population growth. If a more complex quantitative model is to be produced, mortality levels in this period must be more accurately measured. However, qualitative models comparing two or more different control policies may not require accurate measurement of this parameter.

Despite the above limitations, the results of this paper show that it is possible to begin to predict rabbit population growth in England. The variation in the level of fecundity used in the above analysis is much less between years and sites than the yearly variation in the natural mortality rates from one site (Cowan 1987a). The population growth rate is therefore much more dependent on mortality than fecundity, which means that to proceed further it is necessary to quantify the range in variation of natural mortality, if possible broken down to cause, and to calculate the mortality of juvenile rabbits from birth to 4 weeks of age.

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References

Boyce, M.S. (1977) Population growth with stochastic fluctuations in the life table. *Theoretical Population Biology*, **12**, 366−373.

Cowan, D.P. (1987a) Patterns of mortality in a free-living rabbit (*Oryctolagus cuniculus*) population. *Symposium of the Zoological Society of London*, **58**, 59−77.

Cowan, D.P. (1987b) Aspects of the social organisation of the European wild rabbit (*Oryctolagus cuniculus*). *Ethology*, **75**, 197−210.

Cowan, D.P. (1991) The availability of burrows in relation to dispersal in the wild rabbit *Oryctolagus cuniculus. Symposium of the Zoological Society of London*, **63**, 213−230.

Darwin, J.H. & Williams, R.M. (1964) The effect of time of hunting on the size of a rabbit population. *New Zealand Journal of Science*, **7**, 341−352.

Dwyer, G., Levin, S.A. & Buttel, L. (1990) A simulation

model of the population dynamics and evolution of myxomatosis. *Ecological Monographs*, **60**, 423–447.

Joubert, L., Leftheriotis, E. & Mouchet, J. (1972, 1973) *La Myxomatose*, 2 vols. L'Expansion, Paris.

Leslie, P.H. (1945) On the use of matrices in certain population mathematics. *Biometrika*, **33**, 183–212.

Leslie, P.H. (1948) Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**, 213–245.

Lloyd, H.G. (1970) Post-myxomatosis rabbit populations in England and Wales. *EPPO Public Series A*, **58**, 197–215.

Lloyd, H.G. (1981) Biological observations on post-myxomatosis wild rabbit populations in Britain 1955–1979. *Proceedings of the World Lagomorph Conference, Ontario*, pp. 623–628. University of Guelph, Canada.

Marshall, I.D. & Fenner, F. (1958) Studies in the epidemiology of infectious myxomatosis of rabbits. V. Changes in the innate resistance of Australian wild rabbits exposed to myxomatosis. *Journal of Hygiene, Cambridge*, **56**, 288–302.

Marshall, I.D. & Fenner, F. (1960) Studies in the epidemiology of infectious myxomatosis of rabbits. VII. The virulence of strains of myxoma virus recovered from Australian wild rabbits between 1951 and 1959. *Journal of Hygiene, Cambridge*, **58**, 485–487.

Richardson, B.J. & Wood, D.H. (1982) Experimental ecological studies on a subalpine rabbit population. I. Mortality factors acting on emergent kittens. *Australian Wildlife Research*, **50**, 77–95.

Ross, J. (1982) Myxomatosis: the natural evolution of the disease. *Symposium of the Zoological Society of London*, **50**, 77–95.

Ross, J. & Sanders, M.F. (1987) Changes in the virulence of myxoma virus in Britain. *Epidemiological Infection*, **98**, 113–117.

Ross, J. & Tittensor, A.M. (1986) Influence of myxomatosis in regulating rabbit numbers. *Mammal Review*, **16**, 163–168.

Ross, J., Tittensor, A.M., Fox, A.P. & Sanders, M.F. (1989) Myxomatosis in farmland rabbit populations in England and Wales. *Epidemiological Infection*, **103**, 333–357.

Seymour, R.M. (1992) A study of the interaction of virulence, resistance and resource limitation in a model of myxomatosis mediated by the European rabbit flea *Spilopsyllus cuniculi* (Dale). *Ecological Modelling*, **60**, 281–308.

Tittensor, A.M. (1981) Rabbit population trends in southern England. *Proceedings of the World Lagomorph Conference, Ontario*, pp. 629–632. University of Guelph, Canada.

Trout, R.C. & Lelliot, L.M. (1992) Ageing wild rabbits (*Oryctolagus cuniculus*) from Southern England by determining epiphyseal ossification in the lumbar vertebrae. *Journal of Zoology*, **228**, 653–660.

Trout, R.C., Tapper, S.C. & Harradine, J. (1986) Recent trends in the rabbit population in Britain. *Mammal Review*, **16**, 117–123.

Trout, R.C. & Tittensor, A.M. (1989) Can predators regulate wild rabbit *Oryctolagus cuniculus* population density in England and Wales? *Mammal Review*, **19**, 153–173.

Walsingham, J.M., Edelsten, P.R. & Brockington, N.R. (1977) Simulation of the management of a rabbit population for meat production. *Agricultural Systems*, **2**, 85–98.

Wheeler, S.H. & King, D.R. (1985) The European rabbit in South-western Australia III. Survival. *Australian Wildlife Research*, **12**, 213–225.

Wood (1980) The demography of a rabbit population in an arid region of New South Wales, Australia. *Journal of Animal Ecology*, **49**, 55–79.