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The age and post-juvenile growth of rabbits in the south-east of Scotland

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Population structure and adult growth of wild rabbits *Oryctolagus cuniculus* (Linnaeus, 1758) were compared between three habitats, forestry, hill farm and sand dunes, in SE Scotland. The exponentially transformed eye lens weight was used to divide the samples into age classes up to five years old. The forestry and hill farm populations had stable age structures compared with the sand dune population, and the proportion of one year old animals was 58 and 65% compared to only 40% in the sand dunes. The hill farm rabbits were larger than those from the forestry but the pattern of growth was similar. The sand dune rabbits were significantly smaller at all ages and had shorter legs. First year females from the sand dunes were lighter than males of the same age, suggesting that they were not coming into breeding condition, whereas in all the age classes in the other areas, females were heavier than males. It was suggested that the sand dunes rabbits were restricted in growth as a result of poor nutrition.

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Introduction

Rabbits are ubiquitous throughout the British Isles but very little information has been published about how their populations and morphology vary between the different habitats in which they are found (Thompson and Worden 1956, Cowan 1991). Studies in Australia and New Zealand have shown how susceptible the growth of rabbits is to the conditions under which young animals develop (Gibb *et al*. 1978, Myers 1971). Furthermore, individuals are physiologically adult and capable of breeding long before they have completed their growth. Therefore a simple analysis of a sample of adults which does not take their age into account will not provide a reliable description of a population.

During the course of studying the behaviour of rabbits in different areas three samples were trapped at the same time of year (Kolb 1991a, b, 1993). All three came from populations in which there is no winter breeding. In lowland areas the rabbits breeding season can carry on for most of the year (Boyd and Myhill 1987), whereas in upland and arid areas it is much more restricted (Myers 1971). No young rabbits were seen during the winter in any of the areas, and when trapped in March most of the females that were caught were either in oestrus or in the early stages of pregnancy. Therefore these samples allow a matched comparison of the age structure and development of several populations at the crucial period that separates one generation from the next.

Study areas and methods

Samples of rabbits were trapped at three sites in the Lothian and Borders regions of Scotland: (1) Sand Dunes. Trapped 10th–12th March 1987. Altitude < 20 m, rabbit density estimated at 12/ha. (Kolb 1991a). (2) Forestry. Trapped 14th–21st March 1989. Altitude 300–350 m, rabbit density estimated at 2/ha. (Kolb 1991b). (3) Hill Farm. Trapped 13th–15th March 1991. Altitude 300–350 m, rabbit density estimated at 16/ha. (Kolb 1993). More details about each habitat can be found in the above references.

All rabbits were caught in cage traps baited with carrot (Kolb 1993). Each animal was humanely killed, weighed unpaunched and the eyes removed as soon as possible after death. These were fixed in 10% formalin for three weeks. The lenses were then extracted and dried at 80°C for a week before being weighed (Wallage-Drees 1986). The rabbits were autopsied, sexed, and the skull, lumbar vertebrae and femurs removed. They were dried and cleaned using *Dermestes* beetles, with a final boiling in sodium perborate.

Rabbits were separated into three age classes using the degree of fusion of the posterior epiphyses of the lumbar vertebrae (Taylor 1959): (1) those with all the posterior epiphyses open – classified as

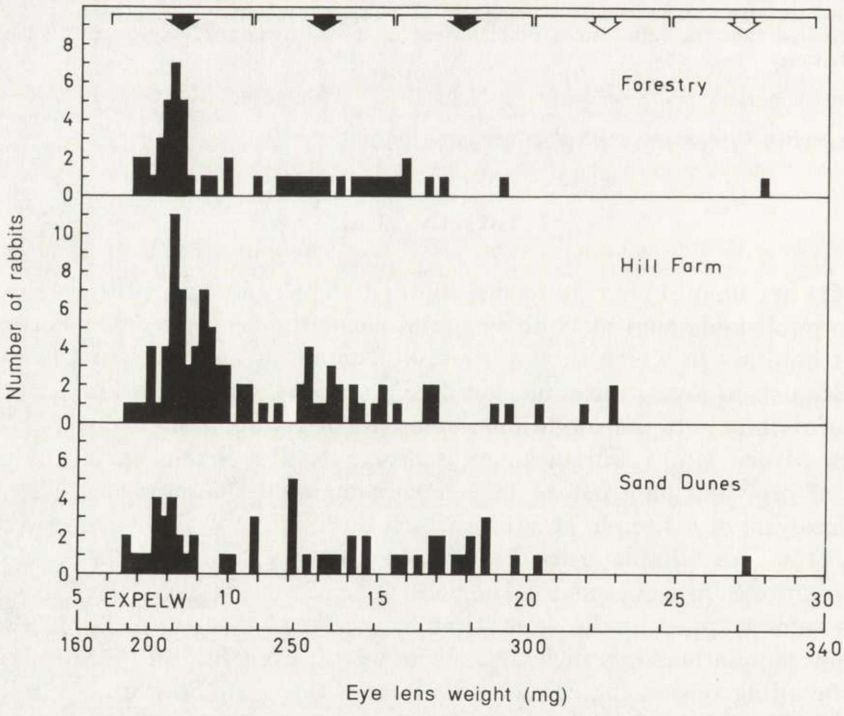

Fig. 1. The transformed eye lens weights (EXPELW) for rabbits from the three habitats. The filled arrows show the mean values for each lumbar vertebrae class with the interpolated cut off points for each age group (for explanation of this procedure see text).

in their first year, (2) those with the 7th or 6th and 7th epiphyses fused – classified as being in their second year, (3) those with all the posterior epiphyses fused – classifed as just under three years old or older.

Standardised growth curves for the eye lens are not available for rabbits in Britain. The growth equations published for Australian rabbits (Myers and Gilbert 1968) do not seem to provide sensible ages from the measurements made in this study, either because of a difference in the technique for preserving the lens or possibly because of inherent differences between Australian and British rabbits. Lloyd (1970) presents a figure for the growth of dried lens weight with age for rabbits from an island in the west of Wales, but provides no mathematical summary that would allow the data to be used. Myers and Gilbert (1968) show that the growth of the lens is exponential for as long as most rabbits are likely to survive. Therefore the weights (in milligrams) obtained in the present study have been transformed as:

$$\text{EXPELW} = e^{(\text{eye lens weight}/100)}$$

This provides a variable which is linear with respect to age, as demonstrated by the almost equal separation of the transformed mean values derived from the lumbar vertebrae age classes (Fig. 1). These values have been extrapolated to later ages and split into equal blocks around the means to provide an approximate breakdown of the number of rabbits in successive age classes within each population (Table 2).

Skull and femur length were measured to the nearest 0.1 mm using a micrometer. Skull length was defined as the greatest distance from the outside of the premaxillae (excluding the incisors) to the rear of the occipital crest. Growth was analysed by plotting body weight on the transformed age variable (Fig. 2). The asymptotic body weight for each population was estimated by fitting a form of the von Bertalanffy growth curve:

$$\text{Weight} = A\ [1 - e^{(-K.\text{Age})}\ ]^3$$

where A is the asymptote and K is a growth constant (Ricklefs 1967). Without the age transformation it is impossible to fit a realistic growth curve to the data as the relationship between body weight and eye lens weight is statistically indistinguishable from a straight line regression. Condition was estimated by dividing body weight by skull length. All calculations of ANOVA and curve fitting were carried out using SYSTAT (Wilkinson 1990).

Results

The mean eye lens weights for each lumbar vertebrae class are shown in Table 1, together with the results from a three way ANOVA. They confirm that growth of the lens is maintained for at least the first three years of life. There are small significant differences between sexes and areas but none of the pairwise comparisons within the age classes are significant, suggesting that the growth of the eye lens is essentially the same in all the areas and is not being affected by local conditions.

In the absence of a single age standard, the lumbar vertebrae classes and the transformed eye lens weight distribution are both presented (Table 2). Where comparison is possible they produce almost the same results. The chief difference between areas is in the percentage of the youngest age class which is much less in the sand dune sample than in the other two habitats. The annual mortality (estimated by the percentage decrease in the number of rabbits in successive age classes) is stable in the two upland populations, averaging about 60% per year.

Table 1. Eye lens weights (mean, SD, and sample size) in mg. F-ratios: Age = 505.0, $p < 0.0001$; Sex = 8.5, $p < 0.01$; Area = 4.8, $p < 0.01$

Area	Sex	Age (yrs) 1	2	3+
Foorestry	M	209 ± 10 (17)	259 ± 12 (9)	281 ± 8 (6)
	F	210 ± 7 (13)	259 ± 10 (6)	333 – (1)
Hill Farm	M	215 ± 10 (36)	256 ± 14 (13)	286 ± 16 (7)
	F	215 ± 13 (22)	261 ± 11 (7)	288 ± 22 (6)
Sand Dunes	M	205 ± 9 (15)	254 ± 14 (10)	290 ± 18 (9)
	F	210 ± 11 (7)	251 ± 12 (6)	286 ± 11 (9)

Table 2. Comparison of the number (n) and mortality (%m) of rabbits in each age class in three habitats, based on the fusion of the lumbar vertebrae (FLV) and the division of transformed eye lens weight into equally spaced segments (TELW). % 1st year: χ^2 (1) = 8.71, χ^2 (2) = 8.00, df = 2, $p < 0.02$.

Area		Age (yrs) 1	2	3(+)	4	5	% 1st year rabbits
FLV							
Forestry	n	30	15	7	0	0	57.7
	%m	–	50	–	–	–	
Hill Farm	n	58	20	13	0	0	63.7
	%m	–	66	–	–	–	
Sand Dunes	n	22	16	18	0	0	39.3
	%m	–	27	–	–	–	
TELW							
Forestry	n	30	15	6	0	1	57.7
	%m	–	50	60	–	–	
Hill Farm	n	59	21	7	4	0	64.8
	%m	–	64	67	–	–	
Sand Dunes	n	23	16	15	1	1	41.1
	%m	–	30	6	–	–	

This is consistent with a small percentage of rabbits surviving until they are five years old. However the mortality estimate from the sand dune population is erratic, with a preponderance of older animals.

Skull length varies significantly with age and area (Table 3). In contrast to eye lens weight, the growth of the skull seems to have stopped by two years of age. Although rabbits from the hill farm had slightly larger skulls than those from the forestry area, the main area difference is with the sand dune rabbits which are smaller at all ages than those from the other areas.

Table 3. Total length of the skull (mean, SD, and sample size) in mm. *F*-ratios: Age = 39.6, $p < 0.0001$; Area = 18.1, $p < 0.0001$; Sex = 1.2, ns.

Area	Sex	Age (yrs)		
		1	2	3+
Forestry	M	78.1 ± 1.6 (17)	79.8 ± 2.2 (9)	80.5 ± 1.6 (6)
	F	77.5 ± 1.5 (13)	79.5 ± 1.4 (6)	81.0 – (1)
Hill Farm	M	78.8 ± 1.7 (36)	81.4 ± 1.8 (13)	81.1 ± 0.8 (7)
	F	77.8 ± 1.5 (22)	80.5 ± 2.1 (7)	81.1 ± 2.0 (6)
Sand Dunes	M	76.9 ± 1.2 (15)	78.8 ± 1.0 (10)	79.3 ± 1.1 (9)
	F	76.5 ± 2.7 (7)	79.0 ± 2.7 (6)	78.7 ± 1.6 (9)

Table 4. Body weight (mean, SD, and sample size) in g. *F*-ratios: age = 62.4, $p < 0.0001$; Area = 38.8, $p < 0.0001$; Sex = 13.4, $p < 0.001$.

Area	Sex	Age (yrs)		
		1	2	3+
Forestry	M	1361 ± 90 (17)	1493 ± 113 (9)	1537 ± 77 (6)
	F	1469 ± 102 (13)	1599 ± 87 (6)	1780 – (1)
Hill Farm	M	1379 ± 94 (36)	1596 ± 113 (13)	1589 ± 119 (7)
	F	1411 ± 103 (22)	1669 ± 142 (7)	1645 ± 81 (6)
Sand Dunes	M	1244 ± 124 (15)	1380 ± 127 (10)	1451 ± 110 (9)
	F	1216 ± 151 (7)	1447 ± 165 (6)	1489 ± 153 (9)

Table 5. Condition – body weight/total skull length (mean, SD, and sample size). *F*-ratios: Age = 50.3, $p < 0.0001$; Area = 34.5, $p < 0.0001$; Sex = 20.0, $p < 0.0001$.

Area	Sex	Age (yrs)		
		1	2	3+
Forestry	M	17.4 ± 1.0 (17)	18.7 ± 1.1 (9)	19.1 ± 0.9 (6)
	F	19.0 ± 1.2 (13)	20.1 ± 1.1 (6)	22.0 – (1)
Hill Farm	M	17.5 ± 1.0 (36)	19.6 ± 1.1 (13)	19.6 ± 1.5 (7)
	F	18.1 ± 1.1 (22)	20.7 ± 1.5 (7)	20.3 ± 0.9 (6)
Sand Dunes	M	16.2 ± 1.5 (15)	17.5 ± 1.6 (10)	18.3 ± 1.2 (9)
	F	15.9 ± 1.7 (7)	18.3 ± 1.7 (6)	18.9 ± 1.7 (9)

Body weight shows a similar pattern to skull growth, with the exception that there are also differences between the sexes (Table 4). In most cases females are

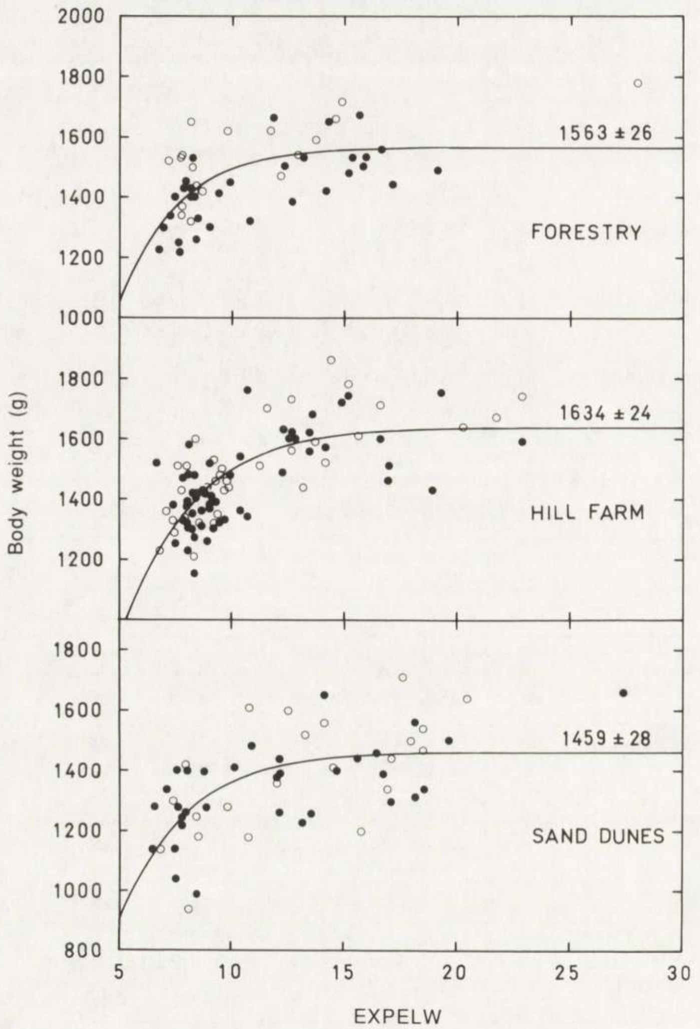

Fig. 2. Plots of body weight on transformed eye lens weight (EXPELW – see text) for rabbits from the three habitats. Fitted von Bertalanffy growth curves are shown with the calculated asymptote for each (± SE). ● – males, ○ – females.

heavier than males, reflecting the fact that they were caught at the start of the breeding season. The exception is with the sand dunes where first year females are lighter than males. This is made even clearer by the measurement of condition (Table 5). The sand dune rabbits are in poorer condition at all ages than those from the other areas, and the first year females are worse than the males, in contrast to the other areas and ages where females outscore males. The calculated asymptotic body weights for each area with the sexes combined, show big differences (Fig. 2). Rabbits from the hill farm are the largest, averaging around 11% more than those from the sand dunes. The latter also produce rabbits with shorter

Table 6. Length of femur (mean, SD, and sample size) in mm. F-ratios: Area = 42.2, $p < 0.0001$; Sex = 3.7, ns; Age = 1.9, ns.

Area	Sex	Age (yrs)		
		1	2	3+
Forestry	M	82.3 ± 1.9 (17)	83.1 ± 1.2 (9)	83.1 ± 2.0 (6)
	F	82.0 ± 1.9 (13)	82.1 ± 1.7 (6)	81.9 – (1)
Hill Farm	M	81.9 ± 1.8 (36)	83.1 ± 1.9 (13)	83.0 ± 1.3 (7)
	F	81.8 ± 1.9 (22)	81.9 ± 1.7 (7)	81.3 ± 2.1 (6)
Sand Dunes	M	79.6 ± 1.2 (15)	80.0 ± 1.3 (10)	78.5 ± 2.6 (9)
	F	79.0 ± 2.2 (7)	80.0 ± 1.3 (6)	79.1 ± 1.0 (9)

femurs at all ages compared to the other two habitats where the lengths are not significantly different (Table 6).

Discussion

Few methods of age determination for animals are error free. The only accurate way is to mark individuals at or near to birth. With eye lens weight most authors agree that first year animals can be reliably distinguished from older ones, but that beyond two years the age classes overlap to some extent as the growth curve flattens out and increases in variability (Myers and Gilbert 1968, Lloyd 1970). With skeletal measurements the extremes of growth are easy to record, but intermediate degrees of epiphyseal fusion can sometimes be difficult to assess. However the two methods used here seem to agree sufficiently to make the classification of most of the age classes reliable.

The two upland populations are quite similar in the proportion of first year animals in the sample and the annual mortality rate up to three years. The main causes of mortality are probably different, with myxomatosis being commonest in the hill farm population, and predation in the forestry area (Kolb 1991b). The sand dune rabbits show completely different characteristics. The proportion of first year animals is low and the age distribution and mortality at later ages is erratic. Each trapping session accounted for a large part of the local population and there was no evidence from the hill farm population that cage trapping selects for different age animals (Kolb 1993). A similar pattern of "centre loading" of the age structure with one and two year old rabbits has been described for arid area populations in Australia by Myers (1971).

Many of the populations of rabbits that have been studied in Australasia have had different body weights. In some instances this has been related to density. In an enclosed population in New Zealand growth rate and body weight were inversely related to the number of rabbits (Gibb *et al.* 1978). Conversely in wild populations sampled in New Zealand body weight was found to be positively related to density (Wodzicki and Roberts 1960). In enclosed populations where numbers are allowed to build up and starvation sets in, growth rate and body weight are depressed, and the size of the ears and feet are smaller than in rabbits growing in more favourable conditions (Myers and Poole 1963). However, where adequate food is available, very high densities do not affect growth and size (Myers 1964). The situation is complicated even more by the fact that selection can produce rabbits with inherited differences in size and the length of the ears and feet. This has already occurred in the regions of Australia, even though rabbits have only been there for less than 150 years (Williams and Moore 1989).

Although the hill farm rabbits are bigger than those from the forestry area, in all other respects they are quite similar despite the big difference in population density. In both areas grazing appeared to be available in surplus throughout the year, so that the larger size of the hill farm rabbits could be an adaption to the more exposed and severe conditions in this habitat. By contrast the rabbits living on sand dunes appeared to run out of food during most winters. The dominant vegetation on the area was marram grass *Ammophila arenaria* L. which rabbits generally avoid eating (Bhadresa 1977). During the summer other grasses and forbs are available (Kolb 1991a) but by the middle of winter these have died down or been eaten. Before grass growth restarts in the spring the rabbits are reduced to nibbling the siliceous stems of dry marram. Many of the features of the population suggest that it is short of food. The growth rate seems to be reduced and the average final body weight and size of the animals is less than in the upland habitats. The rabbits are in a much poorer state, and the first year females do not seem to be coming into breeding condition. While their short legs could be an adaptive feature, they are more likely to be the result of deprivation. The long bones of the limbs are the first parts of the skeleton to mature (Watson and Tyndale-Biscoe 1953) so that they will permanently reflect reduced early growth. In terms of population dynamics the main effect of food shortage on dune areas is to limit reproduction (Wallage-Drees 1983). Outright starvation of adults is rare but since the population is generally near the limits of its food supply, annual variations in the severity of the winter or the length of the growing season can have large effects on the number of rabbits (Wallage-Drees and Michielsen 1989).

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